UNIVERSITÉ DU QUÉBEC À MONTRÉAL

DYNAMIQUE HIVERNALE ET HYPOLIMNÉTIQUE DU CO_2 DANS LES LACS BORÉAUX ET TEMPÉRÉS

MÉMOIRE
PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN BIOLOGIE

PAR
VÉRONIQUE DUCHARME RIEL

JANVIER 2011

REMERCIEMENTS

Je dois commencer par remercier Roxane Maranger qui m'a transmis sa passion pour la limnologie ainsi qu'à son équipe qui m'a enseigné la méthodologie. Tout mon respect à mes directeurs, Paul del Giorgio et Yves Prairie, qui m'ont encouragée et soutenue en tous points. Lisa Fauteux pour tes 101 solutions, ton calme et ton émerveillement, Dominic Vachon, Marie-Eve Ferland et Jérôme Comte pour votre écoute et vos précieux conseils, François Guillemette pour ton positivisme et ta persévérance, Pierre Marcoux pour ton support et ton courage, vous avez été d'une aide indispensable. Merci à Yanick Dessureault, Yanick Dallaire et Jasmin Friolet d'Héli-Inter et Héli Express pour avoir généreusement donné de votre temps pour réparer mon équipement. Toute ma gratitude à Martine Camiré, Annick St-Pierre, Delphine Marchand, Simon Barette, Alice Parks et Catherine Beauchemin qui ont minutieusement recueilli et analysé les données pendant la période estivale. Ma reconnaissance à Robin Bourgeois et Environnement Illimité qui m'ont fournis l'équipement et l'expertise nécessaire à la faisabilité de l'échantillonnage hivernale. Merci à l'équipe de la Station de biologie de l'Université de Montréal pour leur support professionnel et leur accueil. Un gros merci à Alain Tremblay et Hydro Québec pour leur support financier et logistique ainsi qu'au CRSNG et au FQRNT pour le financement. Je n'aurai pu atteindre mes objectifs sans le support et les encouragements de ma famille et de mes amis, merci à tous.

AVANT-PROPOS

La première section du mémoire est une revue de littérature rédigée en français qui met en contexte les connaissances actuelles ainsi que les lacunes concernant le sujet de recherche. Dans la deuxième section, on y présente le premier article (rédigé en anglais) qui étudie la dynamique et les patrons d'accumulation de CO_2 dans les lacs en hiver et dans l'hypolimnion. Dans la deuxième section, on y retrouve le second article (rédigé en anglais) qui porte sur les processus sous-jacents à l'accumulation de CO_2 dans les lacs ainsi que leurs patrons saisonniers. La dernière partie du mémoire est une conclusion en français qui résume les contributions de l'étude. L'échantillonnage a été effectué par moi-même (hiver et période estivale des lacs tempérés) ainsi que par des équipes de terrain (période estivale des lacs boréaux) dirigé par Martine Camiré et Annick St-Pierre. Les analyses et la rédaction des deux articles ont été réalisées en collaboration avec mes directeurs de recherche, soit Paul A. del Giorgio et Yves T. Prairie. Le premier article est soumis à la revue scientifique *Ecosystems* et le second article est soumis à *Limnology and Oceanography.* Par soucis d'économie de papier, toutes les références ont été placées dans une seule section à la fin du document.

TABLE DES MATIÈRES

3. ARTICLE II

LISTE DES FIGURES

Figure Page

Figure Page

LISTE DES TABLEAUX

LISTE DES ABRÉVIATIONS

AHOD	*Areal Hypolimnetic Oxygen Demand*. Taux de diminution de l'oxygène dans l'hypolimnion, exprimé par unité d'aire de surface de l'hypolimnion.
Chl *a*	Concentration en chlorophylle *a* ($\mu g\ L^{-1}$)
CID	Carbone inorganique dissout (mg C L^{-1})
COD	Carbone organique dissout (mg C L^{-1})
$\delta^{13}C$	Signature isotopique du DIC (‰)
$\delta^{13}C$-OC	Signature isotopique du DIC ajouté dans l'hypolimnion, ou dans les lacs couvert de glace (ordonné à l'origine des graphiques de Keeling, en ‰) que l'on assume représenter la signature isotopique du carbone organique respiré.
d	Par jour
DIC	Version anglaise de CID
DOC	Version anglaise de COD
ΔDOC	Diminution de COD dans la colonne d'eau en fonction du temps (mg C m^{-3} d^{-1})
$H\Delta CO_2$	Quantité totale de CO_2 accumulé dans l'hypolimnion (stratification estivale) par unité d'aire de surface du lac (g C m^{-2})
$H\tau\Delta CO_2$	Taux volumétrique d'accumulation de CO_2 dans l'hypolimnion lors de la stratification thermique estivale (mg C m^{-3} d^{-1})
MIMS	Spectromètre de masse à membrane (*membrane inlet mass spectrometer*)
P	Production primaire
PAR	Version anglaise de RAP
pCO_2	Pression partielle de CO_2 (μatm)
PNE	Production nette de l'écosystème

PPB	Production primaire brute
R	Respiration. Dans les articles I et II, R réfère plus précisément à la respiration pélagique.
$\bar{R}$	Respiration pélagique moyenne (mg C m^{-3} d^{-1})
RAP	Radiation active pour la photosynthèse
RQ	Coefficient respiratoire
R_{bent}	Respiration benthique (mg C m^{-2} d^{-1})
std	Standardisation à 10°C des mesures de respiration pélagique ou benthique
TP	Concentration totale de phosphore
$W\Delta CO_2$	Quantité totale de CO_2 accumulé dans un lac couvert de glace (g C m^{-2})
$W\tau\Delta CO_2$	Taux volumétrique d'accumulation de CO_2 dans un lac couvert de glace (mg C m^{-3} d^{-1})
WODR	*Winter Oxygen Depletion Rate*. Taux de diminution de l'oxygène pendant la période du couvert de glace, exprimé par unité de surface du lac.
$\bar{Z}$	Profondeur moyenne

RÉSUMÉ

De nombreux lacs boréaux et tempérés sont maintenant reconnus comme d'importants sites de stockage et d'émissions de carbone, d'où l'intérêt grandissant de déterminer leur rôle à plus grande échelle et d'inclure leur contribution dans les bilans de carbone régionaux. Les lacs tempérés et boréaux de l'hémisphère nord ont souvent deux composantes saisonnières distinctes, soit la période du couvert de glace et la stratification thermique estivale. Dans la littérature, les mesures de CO_2 sont traditionnellement effectuées à la surface des lacs pendant la période libre de glace. Pourtant certaines études suggèrent qu'une quantité importante de CO_2 s'accumule sous la glace et dans l'hypolimnion, c'est-à-dire dans la couche inférieure de la colonne d'eau lors de la période de stratification estivale. Dans la présente étude, nous avons quantifié l'accumulation de CO_2 pendant la période du couvert de glace et dans l'hypolimnion estival de 13 lacs boréaux et de 4 lacs tempérés du Québec et nous avons exploré comment ces accumulations varient dans un gradient de morphométries, de statuts trophiques et de caractéristiques régionales. En deuxième lieu, nous avons étudié la dynamique des processus sous-jacents à l'accumulation de CO_2 pendant la période du couvert de glace et dans l'hypolimnion estival, plus spécifiquement l'importance des processus biotiques, la partition entre la respiration pélagique et benthique, les différentes sources de matière organique supportant la respiration et les coefficients respiratoires à l'échelle de l'écosystème. Nos résultats démontrent que les lacs couverts de glace et l'hypolimnion estival sont des lieus d'accumulation significative de CO_2 puisque considérées ensemble, ces périodes contribuent en moyenne à 33% des émissions annuelles nettes de CO_2 et cette proportion varie selon le statut trophique du lac et la morphométrie. Plusieurs indices recueillis suggèrent que la respiration est la source principale de CO_2 pendant ces deux périodes et que la respiration benthique contribue de façon considérable à la production de CO_2, particulièrement pendant la période du couvert de glace où la respiration benthique est responsable de plus de 50% de l'accumulation totale de CO_2. L'importance relative des sources de matière organique qui alimentent la respiration changent saisonnièrement. Les analyses isotopiques en $\delta^{13}C$ (méthode de Keeling) ont révélées l'importance du carbone organique d'origine planctonique pour alimenter la respiration dans l'hypolimnion alors que les signatures en $\delta^{13}C$ pendant la période du couvert de glace suggèrent une augmentation de l'importance relative de sources terrestres et benthiques.

Mots clefs : Cycle du carbone, émissions de CO_2, métabolisme du lac, couvert de glace, hypolimnion, respiration pélagique, respiration benthique, sources de matière organique respirée, coefficient respiratoire.

1. INTRODUCTION

1.1 L'ÉTUDE DU CARBONE DANS LES ÉCOSYSTÈMES AQUATIQUES

Dans l'Hémisphère Nord, les écosystèmes d'eau douce, qui occupent une portion significative du territoire, ont le potentiel d'influencer le bilan de carbone des écosystèmes terrestres. Contrairement aux océans qui sont reconnus comme des puits de carbone à l'échelle de la biosphère (Denman et al. 2007), les lacs et les rivières sont généralement reconnus comme des sources nettes de carbone vers l'atmosphère (Cole et al. 2007). De façon moindre, les écosystèmes d'eau douce agissent aussi en tant que puits de carbone en stockant annuellement 0,2 Pg C dans leurs sédiments (Cole et al. 2007). Généralement, les lacs qui agissent en tant que source nette de carbone vers l'atmosphère sont qualifiés d'hétérotrophes, ce qui signifie que la respiration totale dans le lac (R) excède la production primaire brute (PPB) résultant en une production nette de l'écosystème (PNE) négative. Traditionnellement, on croit que cette respiration en excès serait majoritairement attribuable aux apports de carbone organique des milieux terrestres vers les milieux aquatiques. Les deux énoncés précédent demeurent toutefois un sujet de débats (Carignan et al. 2000; Dubois et al. 2009; Prairie et al. 2002).

L'inclusion des milieux aquatiques dans les bilans de carbone des écosystèmes terrestres dépend de notre capacité à quantifier et à comprendre la dynamique du carbone dans ces systèmes. Depuis que Cole et al. (1994) ainsi que Kling et al. (1991) ont observé que l'eau de surface des lacs était sursaturée en CO_2, de nombreux travaux ont concentré leurs efforts à estimer le bilan de carbone des lacs et à identifier les mécanismes sous-jacents à cette sursaturation (del Giorgio and Peters 1994; Dubois et al. 2009; Sobek et al. 2003). Dans les régions tempérées froides et boréales, le climat est sujet à d'importantes variations saisonnières qui peuvent faire grandement varier les variables qui modulent la production de CO_2 dans les lacs. Or, la plupart des études sur le carbone sont réalisées pendant la saison libre de glace, à la surface des lacs, période où les échanges gazeux entre le lac et l'atmosphère ont directement lieu. Donc, traditionnellement, deux composantes saisonnières

sont ignorées dans les bilans lacustres de carbone, soit la période du couvert de glace et l'hypolimnion, lors de la stratification thermique estivale. Pourtant, dans de nombreux lacs de l'Hémisphère Nord, ces deux composantes peuvent représenter environ la moitié du cycle annuel des lacs et elles sont potentiellement le lieu d'importantes accumulations de CO_2 (Åberg et al. 2007; Kortelainen et al. 2006).

Le couvert de glace et la stratification thermique forment des barrières physique et thermique empêchant les échanges gazeux entre l'eau et l'atmosphère, favorisant ainsi l'accumulation du CO_2 dans la colonne d'eau. Des études qui ont inclus ces composantes démontrent que le CO_2 s'accumule de façon significative pendant la période du couvert de glace (Kortelainen et al. 2006; Maberly 1996; Striegl and Michmerhuizen 1998) et dans l'hypolimnion, lors de la stratification thermique estivale (Houser et al. 2003; Dillon et Molot 1997). Lors de la fonte de la glace et du brassage automnale, le retrait de ces barrières va donner lieu aux plus importantes émissions de CO_2 dans le bilan annuel des lacs (Striegl et al. 2001), ce qui suggère que la période du couvert de glace et l'hypolimnion pourraient contribuer de façon significative aux émissions annuelles de CO_2.

Par conséquent, les estimations qui n'incluent pas les périodes suivant la fonte de la glace et le brassage automnale sous-estime possiblement les flux annuels de carbone des systèmes lacustres. Afin de pallier à ce manque, ce projet vise à quantifier la contribution de la période du couvert de glace et de l'hypolimnion, lors de la stratification thermique estivale, dans les flux annuel de CO_2 des lacs boréaux et tempérés. Ce projet étudie également plusieurs mécanismes sous-jacents à ces accumulations afin de mieux comprendre la dynamique de ce gaz à effet de serre dans les lacs.

1.2 LES RÉGIONS BORÉALES ET TEMPÉRÉES

1.2.1 La région boréale de l'étude (Région de la rivière Eastmain, Baie James, Qc, Canada)

La forêt boréale québécoise recouvre environ un tiers du territoire (Ministère des ressources naturelles et de la faune du Québec, 2003) et un tiers de sa superficie est composée d'eau douce et de milieux humides (Marchand 2007). L'espèce végétale dominante est l'épinette noire (*Picea mariana*). La moyenne annuelle de précipitations se situe entre 600 et 1200 mm (Ressources naturelles Canada [RNCan], 2007A) et la température moyenne de janvier et de juillet se situent respectivement entre -30 et -15°C (RNCan, 2007B), et entre 6 et 25 °C (RNCan, 2007C). La forêt boréale de la Baie James repose sur un sol principalement rocheux ou de type podzol humo-ferrique (Clayton and Marshall, 1972).

Au Nord du 52^{ième} parallèle, les perturbations des milieux boréaux québécois sont généralement d'ordre naturel (ex. feux de forêts, voir Marchand 2007). Les perturbations d'origine anthropique sont principalement la construction et le maintient de méga-centrales hydroélectriques et la mise en eaux de réservoirs. Au sud du 52^{ième} parallèle, les forêts boréales sont sujettes à l'exploitation commerciale.

1.2.2 Les régions tempérées de l'étude (Laurentides et Estrie, Qc, Canada)

Les régions tempérées de l'Estrie et des Laurentides reçoivent entre 1000 et 2000 mm de précipitations annuellement, dont 30% sont sous forme de neige (Carignan et al. 2000). Les températures moyennes de janvier se situent entre -20 et -5°C (RNCan, 2007B) alors qu'elles varient entre 11 et plus de 25°C en juillet (RNCan, 2007C). La région des Laurentides est située sur des roches intrusives et métamorphiques du bouclier canadien sur lesquelles repose un sol de type podzol humo-ferrique (Clayton and Marshall, 1972). La région de l'Estrie est située à la limite de la plate-forme du Saint-Laurent et des Appalaches. On y retrouve les sols de types podzol humo-ferrique, Brunisol mélanique et Gleysol humique (Clayton and

Marshall, 1972). Les bassins versants des lacs étudiés sont principalement boisés par des peuplements mixtes. Les lacs de l'Estrie sont caractérisés par un pH et une alcalinité élevés (Prairie et al. 2002).

Les perturbations des systèmes lacustres et des forêts dans les régions des Laurentides et de l'Estrie sont principalement d'ordre anthropique. Le déboisement pour la construction de résidences privées et de routes, le rejet des eaux usées domestiques, l'utilisation des lacs à des fins de loisirs nautiques, la présence de centres de villégiature et de camping dans les bassins versants des lacs modifient les apports de nutriments, de polluants et modifient la dynamique de la matière en suspension. On retrouve également la présence d'espèces envahissantes (ex. *Myriophyllum spicatum*) dans plusieurs lacs de ces régions tempérées.

1.3 DYNAMIQUE DU CO_2 DANS LES LACS

1.3.1 Origine du CO_2 lacustre

Les apports externes de CO_2, par exemple via les apports d'eaux souterraines (Striegl and Michmerhuizen 1998) et les tributaires (Dillon and Molot 1997), peuvent contribuer de façon significative aux ajouts de CO_2 dans les lacs. Toutefois, une grande proportion des ajouts de CO_2 aux lacs sont souvent attribuables à des processus internes. La photo-oxydation du carbone organique dissout (COD) en carbone inorganique dissout (CID), c'est-à-dire la dégradation du COD par l'action des U.V., contribue significativement à la production de CO_2 dans les portions de la colonne d'eau où la pénétration des UV (et possiblement de la radiation active pour la photosynthèse) est suffisante (Granéli et al. 1996; Jonsson et al. 2001). La dégradation biologique de la matière organique (respiration) est souvent considérée comme la source principale de CO_2 dans les lacs mais il existe peu d'observations directes supportant cette hypothèse.

1.3.2 Les sources de matière organique

Tel que mentionné précédemment, de nombreuses études suggèrent que la respiration du COD d'origine terrestre est à l'origine de la sursaturation en CO_2 observée dans de nombreux lacs à travers le monde (Åberg et al. 2007; Algesten et al. 2005; Cole et al. 1994; del Giorgio et al. 1997; Hope et al. 1996; Jonsson et al. 2003; Jonsson et al. 2001; Karlsson et al. 2007; Kling et al. 1992; McCallister and del Giorgio 2008; Sobek et al. 2003) mais il s'agit encore d'un sujet de débats (Dubois et al. 2009; Prairie et al. 2002). On peut imaginer que, dans un lac n'ayant aucun apport externe de matière organique, le carbone disponible pour soutenir le métabolisme des hétérotrophes proviendrait du carbone atmosphérique qui a été fixé in situ par les producteurs primaires. La respiration du carbone qui est fixé dans le lac lui-même résulte en un bilan plus ou moins neutre (ou en un bilan de stockage net de carbone si on inclut la sédimentation) entre la fixation du carbone et ça subséquente respiration. Pour qu'un lac puisse respirer davantage de carbone qu'il n'en fixe, il est nécessaire que des apports externes de carbone alimentent cette respiration en excès. Alors, si on assume que le CO_2 est principalement d'origine métabolique, le degré d'hétérotrophie (quand $P < R$) ou de sursaturation en CO_2 d'un lac doit être couplé aux apports de matière organique allochtone (Hanson et al. 2003). On retrouve généralement une relation positive entre la concentration en COD et le niveau de sursaturation ou les émissions de CO_2 (Algesten et al. 2005; Jonsson et al. 2003; Prairie et al. 2002; Sobek et al. 2003), suggérant qu'une partie de ce réservoir de COD est d'origine allochtone et que son utilisation explique les ratios P : R inférieurs à 1.

1.3.3 Influence du bassin versant et de la morphométrie sur la dynamique du CO_2

Les variables morphométriques, les caractéristiques du bassin versant (Sobek et al. 2003) et le climat influencent la relation entre le lac et le milieu terrestre en modulant, entre autres, les apports externes de carbone. Par exemple, on retrouve généralement les pressions partielles de CO_2 (pCO_2) les plus élevées dans les petits lacs (Rantakari and Kortelainen 2005); ces derniers ont généralement un grand ratio de drainage ainsi qu'un court temps de résidence de l'eau et ces caractéristiques sont également associée en soi avec des grandes pCO_2 (Kelly et

al. 2001; Riera et al. 1999; Sobek et al. 2003). La quantité de précipitations reçues pendant la période libre de glace, pouvant influencer les apports externes de carbone par ruissellement (Pace and Cole 2002), est aussi positivement reliée aux émissions annuelles de CO_2 (Rantakari and Kortelainen 2005). L'utilisation des terres et le type de végétation sur le bassin versant peuvent influencer la dynamique des apports externes en carbone et en nutriments, en modifiant leur disponibilité et leur qualité (labilité). Supportant cette idée, les lacs situés sur des bassins versants ayant une grande surface occupée par des tourbières sont souvent plus concentrés en COD (Mattsson et al. 2005) et une plus grande proportion de terres agricoles sur le bassin versant serait possiblement associée à une meilleure qualité de carbone acheminé vers le lac (Mattsson et al. 2005; Rantakari and Kortelainen 2005). De plus, on retrouve des corrélations entre le degré de sursaturation en CO_2 des lacs et les pourcentages de terres agricoles (Kortelainen et al. 2006; Rantakari and Kortelainen 2005) ou de tourbières (Huttunen et al. 2003; Riera et al. 1999; Striegl et al. 2001).

1.3.4 L'effet des nutriments sur la dynamique du CO_2

Dans les lacs boréaux (Kortelainen et al. 2006) et tempérés (Prairie et al. 2002), la concentration en CO_2 des lacs est associée avec la concentration en nutriments (phosphore total et azote total). Étant donné que la respiration (R, qui produit du CO_2) et la production primaire (P, qui consomme le CO_2) sont deux variables positivement associées avec la concentration en phosphore dans les lacs (Hanson et al. 2003; Smith 1979), la forme de la relation entre le phosphore et le CO_2 lacustre peut prendre différentes formes selon l'importance relative de ces deux composantes l'une par rapport à l'autre (ratio P : R). Le ratio P : R varie selon l'étendue de niveaux de productivité des lacs étudiés (del Giorgio and Peters 1994). Également, il est possible que l'effet des nutriments varie entre les lacs selon la structure trophique et les autres limitations (broutage, lumière, autres nutriments) qui peuvent moduler la production primaire et la respiration.

1.4 CARACTÉRISTIQUES DES LACS SOUS LE COUVERT DE GLACE

1.4.1 Hydrologie et échanges gazeux

La présence du couvert de glace a un impact majeur sur la dynamique des lacs. Cette barrière physique empêche la majorité des échanges gazeux entre l'eau et l'atmosphère (Chambers et al. 2008; Wharton et al. 1993) ce qui résulte en une augmentation, au fil de l'hiver, des produits de la respiration et d'une diminution de la disponibilité en oxygène (Baehr and Degrandpre 2002; Chambers et al. 2008) qui peut parfois entraîner une mortalité importante au sein de la communauté ichtyologique (Barica and Mathias 1979). Le couvert de glace minimise les effets du vent et des radiations solaires sur le brassage du lac. Des courants horizontaux (variant de 0,0005 à 0,004 m s^{-1}) causés par des mouvements oscillatoires du couvert de glace générés par le vent ont toutefois été observés (Bengtsson 1996; Petrov et al. 2007).

1.4.2 Profils thermiques

Les profils de température sous la glace suivent un parton de stratification inversée caractérisé par une température plus froide en surface (0,1°C) et une température atteignant 4-5°C près des sédiments (Bengtsson 1996). Les profils demeurent presque constants pendant la durée du couvert de glace (Ellis et al. 1991). Lors de la stratification thermique hivernale, le gradient de température de la colonne d'eau est moins prononcé comparativement au gradient thermique estival (Kortelainen et al. 2006).

1.4.3 Lumière et photosynthèse

Dans les lacs boréaux et tempérés de l'est canadien, la durée du couvert de glace, l'épaisseur de celui-ci ainsi que l'épaisseur de la neige (0,5 à 0,99 m, RNCan, 2009) pendant la période hivernale permettent la formation d'un couvert épais et opaque qui ne laisse pénétrer que très

peu de lumière (voir Chapitre trois, section résultats). Toutefois, l'épaisseur et l'opacité du couvert varient : à la formation du couvert de glace et lors de la fonte partielle de celui-ci, ou encore lors d'hiver plus chaud et plus sec, le couvert de neige est réduit ou absent et la glace est amincie, ce qui permet à la lumière d'atteindre les couches supérieures de la colonne d'eau (Huotari et al. 2009; Karlsson et al. 2008). Dans un lac boréal de Finlande, Huotari et collègues (2009) ont observé des taux de production primaire de 18 à 97 mg C m^{-2} j^{-1} pendant les deux à trois semaines précédent la fonte complète du couvert de glace, ce qui correspond à 16-86% du taux estival moyen observé pour ce même lac sur plusieurs années. Lorsque le couvert est opaque, ce qui est probablement le cas pendant la majeure partie de l'hiver pour les lacs des latitudes nordiques, la production primaire (Chambers et al. 2008; Karlsson et al. 2008) et la photo-dégradation du COD seront très faibles, voire négligeables (Algesten et al. 2005) due à la limitation par la lumière.

1.4.4 Réservoir de matière organique

Si la production primaire demeure très faible pendant la majeure partie de la durée du couvert de glace, les apports de matière organique autochtone fraîchement produite ne constitueront alors pas une source importante de carbone pour alimenter la respiration hivernale. De plus, la barrière physique créée par le couvert de glace isole partiellement le lac de son bassin versant. Les apports de matière organique en provenance des milieux terrestres sont donc faibles (Algesten et al. 2005). Il y a toutefois un acheminement de carbone (principalement d'origine terrestre) vers le lac par les tributaires mais l'importance de ces apports est peu connue (voir les futurs travaux par Vachon et del Giorgio). Une étude en milieu boréal suédois démontre que l'exportation hivernale du carbone organique total (COT) via les ruisseaux correspond à environ 16% de l'exportation annuelle totale de COT d'un bassin versant (Laudon et al. 2004). Le réservoir de matière organique qui alimente la respiration sous le couvert de glace devrait alors être constitué du COD terrestre présent lors de la formation du couvert, du COD acheminé via les tributaires et de la matière organique autochtone qui n'a pas été dégradée pendant la période libre de glace (Karlsson et al. 2008).

1.4.5 Dynamique des nutriments

Dans la colonne d'eau des lacs en hiver, on observe une augmentation des nutriments sous leur forme inorganique. Cette remise en circulation des nutriments inorganiques pourrait être occasionnée par leur faible utilisation par les producteurs primaires (Agbeti and Smol 1995) et par la dégradation des formes organiques.

1.5 DYNAMIQUE DU CO_2 DANS LES LACS COUVERTS DE GLACE

1.5.1 Origine du CO_2 pendant la période du couvert de glace

Le CO_2 produit ou ajouté au lac pendant l'hiver s'accumule dans la colonne d'eau jusqu'à la fonte partielle ou complète du couvert de glace. La dégradation de la matière organique par la respiration des microorganismes est potentiellement une source importante de CO_2 dans de nombreux lacs pendant l'hiver (Algesten et al. 2005; Karlsson et al. 2008). L'absence ou la faible RAP implique que le CO_2 n'est pas consommé significativement par la photosynthèse et que la photo-dégradation de COD est négligeable. L'importance des eaux souterraines demeure peu connue (Striegl and Michemerhuizen 1998) et pourrait varier entre les lacs et régionalement. Les conditions hivernales (gèle des sols, absence de précipitations pluvieuses et faible ruissellement) sur le bassin versant portent à croire que les apports d'eaux souterraines devraient être à leur minimum pendant la période du couvert de glace.

1.5.2 Contribution benthique et pélagique à la production de CO_2

La respiration dans les lacs survient dans les sédiments (respiration benthique) et dans la colonne d'eau (respiration pélagique). Plusieurs études suggèrent que la respiration benthique est une source potentiellement importante de CO_2 pendant la période du couvert de glace (Algesten et al. 2005; Kortelainen et al. 2006; Mathias and Barica 1980; Rantakari and Kortelainen 2005; Welch et al. 1976) mais très peu d'études ont vérifié cette hypothèse de façon directe (Karlsson et al. 2008). Karlsson et collègues (2008) ont observé que 80% de l'accumulation de CID (composé en partie de CO_2) sous le couvert de glace d'un lac subarctique était produit par la respiration dans les sédiments.

1.5.3 Patrons d'accumulation de CO_2 pendant la période du couvert de glace

L'importance du COD sur la dynamique du CO_2 pendant la période libre de glace a été suggérée dans de nombreux travaux (Åberg et al. 2007; Algesten et al. 2005; Cole et al. 1994; del Giorgio et al. 1997; Dillon and Molot 1997; Hope et al. 1996; Jonsson et al. 2003; Jonsson et al. 2001; Karlsson et al. 2007; Kling et al. 1992; McCallister and del Giorgio 2008; Sobek et al. 2003). Comme c'est le cas pour la période libre de glace, on retrouve une association positive entre la concentration en COD et l'accumulation de CO_2 pendant la période du couvert de glace (Kortelainen et al. 2006; Sobek et al. 2003). Rantakari et Kortelainen (2005) ont observé que la pCO_2 dans la colonne d'eau des lacs couverts de glace était plus élevée lorsque cette période était précédée d'un automne pluvieux, la pluie favorisant l'acheminement de COD terrestre vers le bassin lacustre. Les lacs boréaux eutrophes sont associés avec des pCO_2 hivernales plus élevées par rapport à des lacs moins productifs, ce qui pourrait suggérer l'importance, pour la respiration hivernale, des nutriments et/ou de la matière organique autochtone accumulée pendant la période libre de glace (voir aussi Karlsson et al. 2008). Par contre, dans une expérience d'eutrophisation de lacs ontariens, il n'y a pas eu de différences significatives au niveau de l'accumulation de CID totale sous la glace entre les périodes précédant et suivant l'ajout de nutriments dans les lacs

(Schindler 1990), et l'auteur suggère que la respiration pendant la période du couvert de glace serait donc possiblement alimentée par des accumulations à long terme de matière organique.

1.5.4 L'étude du métabolisme des microorganismes hétérotrophes

La respiration est une source potentiellement significative de CO_2 dans les lacs couvert de glace. Donc, les travaux concernant le métabolisme des microorganismes d'eau douce peuvent être une source d'indices utiles à la compréhension des facteurs qui modulent la production de CO_2 pendant cette période. De façon générale, la température est reconnue comme une variable aillant une influence considérable sur les taux métaboliques des microorganismes aquatiques (Apple et al. 2006; Nedwell 1999; Simon and Wünsch 1998; White et al. 1991). Des études en laboratoire ont démontré que des ajouts de nutriments et de glucose dans des incubations à court terme accéléraient les taux métaboliques mais que de faibles températures (<11°C) avaient tendance à estomper l'effet de ces ajouts (Carlsson and Caron 2001; Granéli et al. 1996; Tulonen 1993). Extrapolés à l'échelle du système, ces résultats pourraient suggérer une limitation première par la température en hiver, lors du couvert de glace, étant donné la faible température de la colonne d'eau. L'effet de la variation en nutriments entre les lacs pourrait alors être estompé par l'effet de la température.

Les résultats de Carlsson et Caron (2001), Granéli et collègues (1996) et de Tolunen (1993) démontrent un effet direct et à court terme des nutriments sur les taux métaboliques. À l'échelle d'un lac, la disponibilité en nutriments pourrait aussi avoir des effets indirects et à long terme (non-observables dans des incubations en laboratoire). Par exemple, la différence de statut trophique pourrait faire varier la disponibilité en matière organique autochtone. Si la matière organique autochtone produite pendant la période libre de glace n'est pas entièrement dégradée avant le début de la période du couvert de glace, cette source pourrait potentiellement alimenter une partie de la respiration hivernale (Karlsson et al. 2008). La matière organique d'origine autochtone est reconnue comme une source plus labile pour les microorganismes, par rapport à certains autres types de carbone plus réfractaires. Les sources et la disponibilité de la matière organique sont des variables à considérer pendant la période

du couvert de glace étant donnée que plusieurs observations suggèrent que la limitation par la température pourrait être partiellement contrée par une grande disponibilité en nutriments et en matière organique labile (Crump et al. 2003; Tulonen 1993). Supportant cette idée, Cotner et collègues (2000) ont observé des taux de production bactérienne pélagique à une température de 2°C, qui correspondaient à 64% de ceux observés pendant l'été, lors d'un épisode hivernal de remise en suspension des sédiments (riches en nutriments et matière organique). Lorsque les lacs sont couverts de glace, la période de plus grande disponibilité en matière organique devrait être en début de saison alors que la période de plus forte disponibilité en nutriments inorganiques serait possiblement en fin de saison. Plusieurs études ont observé que les taux de consommation d'oxygène (respiration) sont plus élevés au début de la période du couvert de glace et qu'ils diminuent au fils de l'hiver (Chambers et al. 2008; Mathias and Barica 1980), suggérant que la disponibilité en matière organique pourrait être une variable importante dans la modulation de la production du CO_2 sous le couvert de glace.

1.5.5 Contribution de la période du couvert de glace aux bilans annuels de CO_2 des lacs

La contribution de la période du couvert de glace aux flux annuels de CO_2 des lacs est peu connue, l'hiver demeurant une saison très peu étudiée. La période du couvert de glace a le potentiel d'augmenter le degré d'hétérotrophie des lacs puisque, pendant cette période, la respiration devrait être nettement supérieure à la photosynthèse, cette dernière étant limitée par la lumière. Comme le démontre des études effectuées sur plus de 200 lacs boréaux (Kortelainen et al. 2006; Rantakari and Kortelainen 2005) et tempérés (Dillon and Molot 1997) de différentes tailles, les quantités de CO_2 (ou de CID) lacustres les plus élevées sont observables pendant la période du couvert de glace. En moyenne, la pCO_2 correspondait à 10 fois la valeur à saturation (Kortelainen et al. 2006), ce qui suggère des accumulations significatives de CO_2 sous le couvert de glace.

Le CO_2 accumulé pendant la période du couvert de glace est expulsé rapidement vers l'atmosphère dans les quelques jours suivant la fonte du couvert (Huotari et al. 2009; Striegl et al. 2001; Striegl and Michmerhuizen 1998) et les émissions qui en résultent sont

potentiellement significatives dans le bilan annuel des lacs (Striegl et al. 2001). La moitié des émissions printanières de CO_2 auraient lieu dans le premier jour suivant la fonte de la glace (Striegl and Michmerhuizen 1998). Les émissions printanières représenteraient de 1 à 18% des émissions annuelles de CO_2 de lacs oligotrophes à mésotrophes de différentes régions de l'Hémisphère Nord (Algesten et al. 2003; Huotari et al. 2009; Rantakari and Kortelainen 2005; Riera et al. 1999; Striegl and Michmerhuizen 1998). Dans un petit lac subarctique de Finlande, Karlsson et collègues (2008) ont montré qu'environ un quart (26%) de la respiration annuelle totale du lac se produisait pendant la période du couvert de glace.

1.6 CARACTÉRISTIQUES DE L'HYPOLIMNION

1.6.1 Définition de l'hypolimnion estival (Lacs Dimictiques)

À la fin du printemps ou au début de l'été, le réchauffement de l'air provoque une augmentation de température dans les eaux de surface du lac. L'eau plus chaude et moins dense va demeurer en surface alors que l'eau plus froide qui se trouve au fond du bassin lacustre ne sera plus mélangée avec la masse d'eau en surface. Entre ces deux masses d'eau se forme un gradient important de température et de densité de l'eau que l'on nomme la thermocline. La masse d'eau où est située la thermocline se nomme le métalimnion. C'est la thermocline qui agit en tant que barrière thermique. Sa présence minimise les interactions entre l'hypolimnion (masse d'eau inférieure) et l'épilimnion (zone de mélange de surface). En automne, lorsque la température de l'air se refroidit, la température de l'épilimnion va aussi refroidir, ce qui va diminuer le gradient de densité de l'eau et fragiliser la stratification thermique. Avec l'action des vents et des mouvements convectifs de l'eau, le métalimnion va graduellement être mélangé avec l'épilimnion jusqu'au mélange complet de la colonne d'eau (mélange automnal).

1.6.2 Lumière et photosynthèse

Dans les lacs ayant une forte concentration en COD (Houser et al. 2003) ou dans les lacs très productifs, le pourcentage de lumière incidente à atteindre les couches supérieures de l'hypolimnion est inférieur à 1%. Par contre, dans les lacs ayant une plus faible concentration en COD, la profondeur à laquelle il est possible de mesurer 1% ou plus de lumière incidente peut se retrouver sous la thermocline (Houser et al. 2003). Dû à la limitation par la lumière, la production primaire et la photo-dégradation du COD devraient être généralement faibles dans l'hypolimnion.

1.6.3 Réservoir de matière organique

La thermocline ralentit les échanges de matière dissoute entre les couches de surface du lac et l'hypolimnion. La majorité de COD terrestre qui est acheminé vers le lac (ex. tributaires) pendant la période de stratification n'atteindra pas l'hypolimnion (Houser et al. 2003). Alors, le COD disponible pour la respiration hypolimnétique est celui qui était présent au moment de la formation de la stratification thermique. Houser et collègues (2003) ont observé une diminution du COD dans l'hypolimnion en fonction du temps suggérant que le COD est utilisé en tant que source de matière organique pour la respiration. Bien que la production primaire puisse être relativement faible dans l'hypolimnion par rapport aux couches de surface qui reçoivent davantage de lumière, 10 à 50% de la matière organique autochtone produite dans le métalimnion et l'épilimnion est exportée dans l'hypolimnion par sédimentation des formes particulaires (Baines and Pace 1994). Le flux de matière organique particulaire vers l'hypolimnion est positivement relié à la concentration totale de pigments dans le métalimnion (Baines and Pace 1994). Il peut également y avoir des migrations verticales et des pics d'abondance de phytoplancton sous la thermocline. Le réservoir de matière organique dans l'hypolimnion devrait donc être constitué du COD présent lors de formation de la stratification et d'apports de matière organique autochtone.

1.7 DYNAMIQUE DU CO_2 DANS L'HYPOLIMNION

1.7.1 Processus aérobiques et anaérobiques

La diffusion des gaz entre l'hypolimnion et les masses d'eau de surface est faible (Bédard and Knowles 1991; Cornett and Rigler 1987; Houser et al. 2003). Les produits de la respiration vont s'accumuler dans l'hypolimnion jusqu'au brassage automnale de la colonne d'eau. La consommation d'oxygène dans l'hypolimnion peut donner lieu à des conditions anoxiques dont l'occurrence varie en fonction de la concentration en nutriments, de la morphométrie du lac, de l'épaisseur de l'hypolimnion, de la température de l'eau (Charlton 1980; Molot et al. 1992; Nürnberg 1995) et de la durée de la stratification thermique. La sédimentation de matière organique particulaire en provenance des masses d'eau de surface est aussi associée à une plus grande consommation d'oxygène dans l'hypolimnion (Matthews and Effler 2006). Lorsque des conditions anoxiques surviennent, le métabolisme de l'hypolimnion va être dominé par des processus anaérobiques. Les principales réactions d'oxydoréduction qui produisent du CO_2 dans l'hypolimnion sont les suivantes (Houser et al. 2003) :

A) Respiration aérobique: $CH_2O + O_2 \rightarrow CO_2 + H_2O$

B) Oxydation aérobique du méthane : $CH_4 + 2O_2 \rightarrow CO_2 + 2H_2O$

C) Dénitrification: $1{,}2CH_2O + HNO_3 \rightarrow 1{,}25\ CO_2 + 0{,}5\ N_2 + 1{,}75\ H_2O$

D) Réduction du sulfate : $2CH_2O + SO_4^{2-} + H^+ \rightarrow HS^- + 2H_2O + 2CO_2$

E) Méthanogénèse : $CH_3OOH \rightarrow CH_4 + CO_2$

1.7.2 Contribution benthique et pélagique à la production de CO_2

Le CO_2 produit par les processus métaboliques dans l'hypolimnion peut provenir des sédiments et de la colonne d'eau. Les données recueillies dans une revue de littérature sur la respiration par Pace et Prairie (2005) suggèrent que la respiration dans les sédiments est responsable de 30 à 80% de la consommation totale d'oxygène dans l'hypolimnion de lacs

tempérés (voir aussi Cornett and Rigler 1987). Dans un grand lac humique de Suède, 40% de l'accumulation de CO_2 était attribuable à sa production dans les sédiments (Jonsson et al. 2001).

1.7.3 Sources de matière organique

Plusieurs études suggèrent que le COD, constitué en grande partie de carbone terrestre, est une source importante de matière organique qui alimente la respiration dans l'hypolimnion (Algesten et al. 2005; Jonsson et al. 2001). L'accumulation de CID dans l'hypolimnion, lors de la stratification thermique estivale, est reliée à une diminution en COD (Houser et al. 2003). Dans l'hypolimnion estival d'un lac subarctique de Finlande, la quasi-totalité de la respiration était supportée par du carbone d'origine terrestre (Åberg et al. 2007). La concentration en nutriments (phosphore et azote), qui fait varier les taux de production primaire dans les couches d'eau de surface, est aussi positivement reliée aux taux de respiration dans l'hypolimnion (Nürnberg 1995). La matière organique particulaire provenant de la production primaire en surface qui sédimente dans l'hypolimnion (Baines and Pace 1994) pourrait être une source de matière organique importante pour le métabolisme hypolimnétique. McCallister et del Giorgio (2008) ont démontré que, dans l'épilimnion, la proportion de matière organique autochtone respirée augmenterait en fonction du statut trophique du lac et cette observation pourrait possiblement s'appliquer à l'hypolimnion.

1.7.4 L'étude du métabolisme des microorganismes hétérotrophes

Les taux de respiration planctonique dans l'hypolimnion estival sont plus lents que dans les couches d'eau de surface (Åberg et al. 2007). Dans le lac Memphrémagog où la profondeur maximale est d'environ 100 mètres, la respiration hypolimnétique correspondait à environ 4% de la respiration épilimnetique (Cornett and Rigler 1987; del Giorgio and Peters 1994; Pace and Prairie 2005). La respiration planctonique dans l'hypolimnion d'un lac subarctique correspondait à environ 40% de la respiration dans l'épilimnion et le métalimnion (Åberg et

al. 2007). La différence de température entre les masses d'eau pourrait être majoritairement responsable de la variation entre les taux de surfaces et les taux hypolimnétiques.

1.7.5 Contribution de l'hypolimnion aux bilans annuels de CO_2 des lacs

La contribution de l'hypolimnion estival aux émissions annuelles nettes de CO_2 est très peu connue. Le brassage automnal, qui remet le CO_2 accumulé dans l'hypolimnion en circulation dans la colonne d'eau, est toutefois associé avec les flux qui sont parmi les plus élevés de l'année (Riera et al. 1999). Une accumulation importante de DIC ou de CO_2 survient dans l'hypolimnion estival (Dillon and Molot 1997; Houser et al. 2003; Jonsson et al. 2001; Riera et al. 1999; Striegl and Michmerhuizen 1998) et pourrait mener à d'importantes émissions de CO_2 lors de la période de brassage automnal.

1.8 OBJECTIFS ET HYPOTHÈSES

Très peu de travaux ont suivi la dynamique du CO_2 des lacs dans un cycle annuel complet et les études concernant le métabolisme sous le couvert de glace sont particulièrement rares dans la littérature scientifique. Les bilans annuels de CO_2 qui n'incluent pas les émissions résultant de l'accumulation sous le couvert de glace et dans l'hypolimnion estival sous-estiment les émissions annuelles de carbone des lacs. Étonnamment, presque aucune étude n'a étudié l'hypolimnion estival et la période du couvert de glace l'un par rapport à l'autre. Pourtant, la présence de ces deux périodes naturelles d'isolation fournit un contexte favorable à l'étude de l'accumulation de CO_2 et aux comparaisons saisonnières in situ pour un même lac. L'étude de ces deux composantes du cycle annuel pourrait être une source d'informations utiles à la compréhension de la dynamique saisonnière de la production de gaz à effet de serre dans les lacs.

Ce projet porte sur la dynamique du CO_2 de 12 lacs boréaux et de 4 lacs tempérés dans un cycle annuel complet, en incluant la période du couvert de glace et l'hypolimnion. Les lacs

ont été sélectionnés pour obtenir un gradient trophique et différentes morphométries. Le premier volet de cette étude vise à quantifier l'accumulation de CO_2 en hiver et dans l'hypolimnion estival afin de connaître leur contribution au bilan de carbone annuel des lacs. Les sous-objectifs de ce premier volet sont d'étudier les patrons d'accumulation de CO_2 dans un gradient trophique, de comparer les patrons d'accumulation de la période du couvert de glace et de l'hypolimnion estival et de fournir des outils empiriques permettant d'inclure des accumulations hivernales et hypolimnétiques de CO_2 aux les bilans annuels de carbone des lacs. Le second volet de cette étude à pour but d'étudier les mécanismes sous-jacents à l'accumulation de CO_2 dans les lacs et leur dynamique saisonnière, c'est-à-dire la contribution des processus biotiques, la respiration pélagique, la contribution de la respiration benthique, les sources de matière organique utilisées (terrestre versus algal) et le couplage entre la production de CO_2 et la consommation d'oxygène (Coefficient Respiratoire) à l'échelle du lac.

Les mesures de CO_2 sous le couvert de glace et dans l'hypolimnion ont été effectuées in situ sur une base mensuelle selon la méthode de Cole et Prairie (2009) puisque cette méthode est facilement utilisable en région éloignée et qu'elle offre la précision recherchée. La respiration pélagique a été mesurée à partir de la diminution en O_2 dans des incubations effectuées à la noirceur, selon les méthodes suggérées dans del Giorgio and Bouvier (2002; spectromètre de masse à membrane) et Marchand (2007; système d'optrode, voir Chapitre 3, section Methods pour une description détaillée des méthodes utilisées), qui offrent respectivement des avantages différents en termes de logistique et de précision. La contribution de la respiration benthique a été estimée par différence à partir de l'accumulation totale de CO_2 (sous le couvert de glace ou dans l'hypolimnion) et la respiration pélagique de la période correspondante. Les sources de carbones utilisées pour la respiration ont été estimées à partir des isotopes stables de carbone ($\delta^{13}C$) en utilisant les graphiques de Keeling (Karlsson et al. 2007; Keeling 1958). Les coefficients respiratoires ont été estimés à l'échelle du lac en utilisant des régressions orthogonales entre les distances par rapport aux valeurs à saturation des concentrations de CO_2 et d'O_2 provenant de profils verticaux effectués à des temps donnés.

La saison estivale étant généralement beaucoup plus active, on s'attend à ce que l'hypolimnion estival accumule une plus grande quantité de CO_2 que les lacs en hiver, malgré un volume d'eau plus important sous le couvert de glace par rapport au volume hypolimnétique. Les lacs sont beaucoup plus similaires entre eux en hiver qu'en été puisqu'ils sont tous limités par la lumière et la faible température de l'eau. On pourrait observer un découplage entre l'accumulation de CO_2 sous la glace et les nutriments ou la concentration en COD puisque la température semblent estomper l'effet de la disponibilité des nutriments et de la matière organique dans certaines études réalisées en laboratoire (Carlsson et Caron 2001; Félip et al. 1996). Malgré la faible intensité lumineuse dans l'hypolimnion, la production primaire en surface (Baines and Pace 1994) peut influencer le métabolisme de l'hypolimnion, on s'attend donc à ce que l'accumulation de CO_2 hypolimnétique soit positivement couplée au statut trophique du lac. La respiration pélagique devrait être plus faible en hiver que dans l'hypolimnion étant donné l'importante influence de la température sur les taux métaboliques (Apple et al. 2006). Il est possible que les sédiments, qui sont beaucoup plus riches que la colonne d'eau en nutriments et en matière organique, puissent soutenir des taux plus élevés de respiration et ce, même pendant la période du couvert de glace. Le ralentissement anticipé des processus biologiques dans la colonne d'eau pendant l'hiver pourrait faire en sorte qu'on observe une contribution relative des sédiments plus grande pendant la période du couvert de glace (Åberg et al. 2007). Également, on anticipe un changement dans les sources de matière organique qui alimentent le métabolisme des microorganismes entre la période du couvert de glace et l'hypolimnion puisque la disponibilité de la matière algale devrait être relativement faible en hiver étant donnée la limitation de la production primaire par la lumière. Le métabolisme hivernal devrait donc être alimenté principalement par des sources de carbone moins labiles (surtout d'origine terrestre) qui n'auront pas été consommées pendant la période libre de glace.

2. ARTICLE I

THE CONTRIBUTION OF WINTER UNDER-ICE AND SUMMER HYPOLIMNETIC CO_2 ACCUMULATION TO THE ANNUAL CO_2 BUDGET OF TEMPERATE AND BOREAL LAKES IN QUÉBEC[1]

Ducharme-Riel, Véronique[2], Yves T. Prairie[2] and Paul A. del Giorgio[2]

This paper is submitted to the journal *Ecosystems*.

Authors contributions:

VDR: Designed the study, sampling, analysed the data and wrote the paper.

YTP: Conceived and designed the study, analysed the data and wrote the paper.

PAdG: Designed the study, analysed the data and wrote the paper.

[1] All sited references are grouped in a single reference section at the end of the thesis.

[2] Département des Sciences Biologiques, Université du Québec à Montréal, Case Postale 8888, succursale Centre-Ville, Montréal, QC, H3C 3P8, Canada.

2.1 ACKNOWLEDGEMENTS

We wish to thank Lisa Fauteux, Marie-Eve Ferland, François Guillemette, Pierre Marcoux, Martine Camiré, Annick St-Pierre, Jérôme Comte and Environnement Illimité for field support, and Catherine Beauchemin and Alice Parks for help in the lab. Thanks to Jean-François Hélie and Roxane Maranger for their advice during project planning. This research was supported by funds from the Environmental Division of Hydro Québec through the Eastmain-1 Project, the Natural Sciences and Engineering Research Council of Canada (NSERC), and by the Quebec fund for natural sciences and technologies (FQRNT) through a graduate scholarship to VDR.

2.2 ABSTRACT

Northern lakes are now recognized as important sites of both C storage and C emission to the atmosphere, and there is increasing interest in determining their role in regional C budgets. The annual CO_2 budget of northern lakes has very distinct seasonal components: lakes are covered by a thick layer of ice during more than three months per year and are thermally stratified during summer. Here we explore the whole-lake accumulation of CO_2 during winter ice-cover, and in the hypolimnion during summer stratification, in temperate and boreal lakes in Québec, and how these processes vary with lake trophic state, morphometry and regional characteristics. We have further followed surface pCO_2 during the open water season and have estimated an annual CO_2 budget for each lake that incorporates the fluxes resulting from winter ice-cover and summer hypolimnetic CO_2 accumulation to explore their relative importance. The volumetric rates of CO_2 accumulation during the winter ice-cover ranged from 3.5 to 24.5 mg C m^{-3} d^{-1}, and varied as an inverse function of mean lake depth. The CO_2 accumulation rates in the summer hypolimnia ranged from 2.1 to 39 mg C m^{-3} d^{-1} and were positively related to TP. The resulting total areal CO_2 accumulation during winter ice-cover varied from 4 to 14 g C m^{-2}, and was on average higher and considerably less variable than the areal hypolimnetic CO_2 accumulation for the same lakes, which ranged from 0.3 to 11 g C m^{-2}. The annual CO_2 emission rates in these lakes ranged from 25 to 56 g C m^{-2} y^{-1}, and were positively related to DOC concentration and negatively related to lake area. The winter ice-cover CO_2 accumulation accounted from 7 to over 50% of the annual CO_2 efflux from the lakes, whereas summer hypolimnetic accumulation accounted on average for less (from 1 to 44%). Our results suggest that winter and summer hypolimnetic C accumulation are important components of northern lake C budgets, and confer stability to the total annual C cycle in these systems.

Key words: Carbon, CO_2, winter, hypolimnion, lake carbon budgets, temperate, boreal

2.3 INTRODUCTION

Since the observation made by Kling and others (1991) and Cole and others (1994) that most northern lakes are supersaturated in CO_2, and are thus net sources of carbon to the atmosphere, many studies have focused on understanding the patterns and processes underlying these emissions. There are now some well-established patterns in CO_2 supersaturation across lakes, for example, in relation to lake morphometry (Kelly and others 2001; Rantakari and Kortelainen 2005), DOC concentration (Sobek and others 2003), nutrients (Kortelainen and others 2006), chlorophyll concentration (Praire 2008; Roehm and others 2009), and catchment characteristics (Sobek and others 2003; Kortelainen and others 2006). There is also increasing evidence that the resulting lake CO_2 emissions are significant at a whole-landscape level, especially in water-rich northern regions (Algesten and others 2003; Kortelainen and others 2006). Lake CO_2 dynamics are strongly coupled to the external loading of nutrients, organic (Hope and others 1996; Algesten and others 2003) and inorganic carbon (Dillon and Molot 1997), and to autochthonous primary production (del Giorgio and Peters 1994), which are in turn linked to regional climatic and hydrologic variables. Northern lakes in particular are subject to strong seasonal variations in these characteristics, yet traditionally, studies on lake CO_2 dynamics have focused on the open water season, and often target only the surface layers of lakes. Winter processes, especially in ice-covered lakes, as well as C dynamics that occur in the deeper layers of stratified lakes in summer have been much less extensively studied. In particular, these components of lake C dynamics have seldom been integrated into the annual C budget of lakes, and this gap may be particularly significant in Northern temperate and boreal landscapes, which have both a long ice-cover period in winter, and a summer stratification that lasts for several months.

Winter under-ice and summer hypolimnetic C dynamics have typically been studied separately. There have been a number of studies that have explored CO_2 dynamics under the ice in lakes, and have reported significant rates of CO_2 accumulation (Riera and others 1999; Striegl and others 2001). Other studies have focused not on CO_2 per se, but on O_2 dynamics under the ice, especially in the context of winter fish kills (Welch and others 1976; Mathias and Barica 1980; Babin and Prepas 1985). The handful of studies that have directly (Maberly

1996; Kortelainen and others 2006; Huotari and others 2009) or indirectly (Striegl and others 2001) quantified winter lake CO_2 accumulation, all tend to suggest that under-ice CO_2 build up may be significant in terms of the annual budget. However, how these rates of winter C accumulation vary with lake and watershed properties, and across regions, has yet to be investigated.

Likewise, previous studies have shown that the accumulation of CO_2 in the summer hypolimnia of stratified lakes may also be significant (Striegl and Michmerhuizen 1998; Riera and others 1999; Houser and others 2003) and results in large CO_2 evasion during fall mixing. Similarly to the studies on winter metabolism, more studies of summer hypolimnia have focused on the O_2 depletion to assess the impacts of anthropogenic eutrophication and potential impacts on fish and on sediment biogeochemistry (Charlton 1980; Cornett and Rigler 1987; Matthews and Effler 2006).

It is clear that in order to assess the regional role of northern lakes, it is necessary to effectively quantify the annual lake C budgets, and this in turn requires the integration of all potentially significant components of this budget, including both winter under-ice and summer stratification processes. While there is some existing information on these components individually for a variety of lakes, what is almost completely lacking is insights on how winter and summer hypolimnetic CO_2 dynamics compare within the same lakes, in terms of their respective magnitudes, and their cross-lake and regional patterns. There are some analogies, but also major differences in C dynamics between summer stratification and winter ice cover, such that it is difficult, if not impossible to extrapolate one from the other. In this study, we explored CO_2 dynamics under the ice and in the summer hypolimnia of lakes in three distinct temperate and boreal regions of Québec that differ in climate, geology and land-cover; we quantify the magnitude of winter ice-cover and summer hypolimnetic CO_2 accumulation, explore patterns of accumulation relative to lake morphometry, chemistry and watershed properties, and quantify the contribution of these components to the annual lake CO_2 emissions, and how this contribution varies across of these boreal and temperate lakes.

2.4 METHODS

2.4.1 Study sites and sampling design

For this study we targeted a total of 16 lakes, within two broad regions (Figure 2.1). Four lakes were sampled in the southern temperate region of Québec: Two of these (Bowker and Bran de Scie) are located in the Appalachian area of Eastern-Townships, 150 km south of Montréal, and the other two (Croche and Connelly) are located in the Laurentian area of the Canadian Shield, 100 km North of Montréal; twelve lakes were further sampled in the Eastmain River region of boreal Québec, approximately 1500 km Northwest of Montréal. The two regions, boreal and temperate, are characterized by large differences in climate: Average January temperatures range from -30 to -15°C and from -20 to -5°C, respectively, and the length of lake ice cover is on average 180 and 140 days respectively. Average June temperatures in the boreal region range from 6 to 25 °C and from 11 to over 25 °C in the temperate region (Natural Resources Canada, 2007B and C). Lakes were selected within each region to obtain a range of nutrient concentrations and morphometry (Table 2.1), similar between both temperate and boreal regions.

2.4.2 Sampling

The four lakes in the temperate region were sampled monthly during an annual cycle, from Nov. 2007 to Nov. 2008. The twelve boreal lakes were also followed over an annual cycle but the sampling interval varied: They were sampled in June, July/August and September of both 2007 and 2008 (spring/summer samples), and in December 2007 and March 2008 (winter samples). Lakes were visited once during each sampling month, at their deepest and central point.

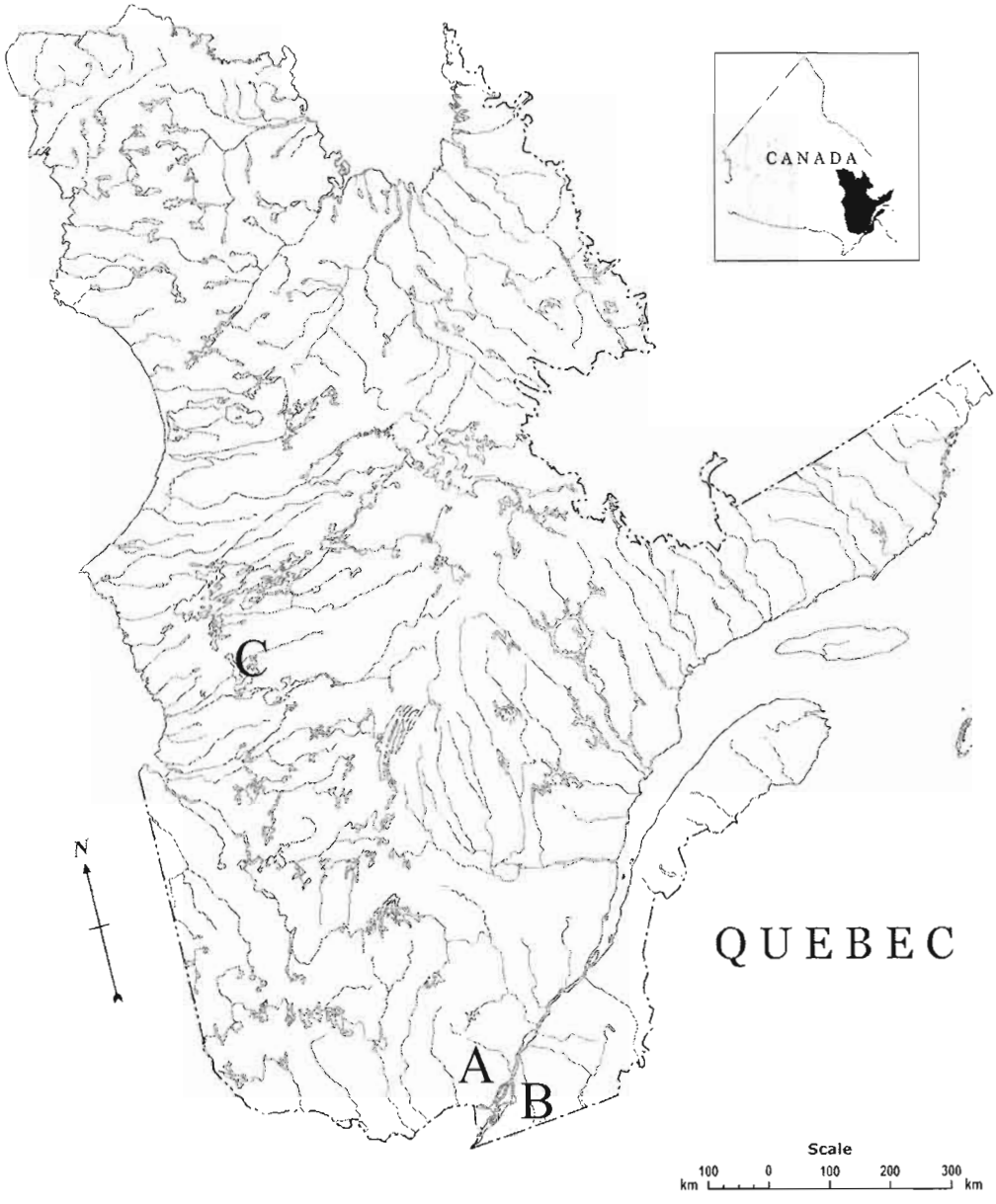

Figure 2.1 Map of Québec showing the geographical position of (A) the Laurentian region (Lake Croche and Connelly), (B) the Eastern-Townships region (Lake Bowker and Bran de Scie) and (C) the Eastmain River region (boreal lakes). This map was reproduced with the permission of Natural Resources Canada 2010, from the Atlas of Canada.

The percentage of incident light penetrating the ice cover, as well as the light attenuation profile during the open water period was determined with a Li-Cor (Li-1400, quantum underwater cell 6574). During the ice cover period, the Li-Cor underwater probe was placed under the ice cover via a hole drilled in the ice and the incident light probe was kept over the ice and snow cover. Secchi depth was further measured for all lakes during the open water period. A detailed depth profile (one meter interval) of temperature, pH, conductivity, O_2 (using a YSI 600XLM, Yellow Spring Instruments Inc.), and pCO_2 was carried out at each sampling time. In situ pCO_2 was determined using an EGM-4 (PP Systems Inc.) connected to a gas equilibrator (Mini Module membrane contactor G542, Membrane Underlining Performance Inc.) in a closed recirculating loop and a peristaltic pump (see Cole and Prairie 2009). At the outlet of the peristaltic pump, a Y-shaped connection allowed the water to pass through the gas equilibrator for pCO_2 measurements or through a length of tubing to collect other types of samples at the desired depths. Water samples were collected at a 1 meter depth for total phosphorus (TP), dissolved organic carbon (DOC) and chlorophyll *a*. All tubes were acid washed and rinsed three times with nanopure and in situ water before filling. Water for DOC was filtered through a 0.45 µm Sarstedt Filtropur capsule using a syringe. Samples were kept colder than in situ temperature during transport to the lab to avoid further formation of bubbles. In the lab, the samples were stored at 3°C until analysis. DOC samples were run in an O.I. Analytical 1010 TIC-TOC analyser. TP was analysed with unfiltered water after persulfate digestion, and chlorophyll *a* was extracted in ethanol. The tubes were submersed in a water bath at 78°C during 10 minutes and were then kept at 4°C during 24 hours prior to analysis. Chlorophyll *a* concentration was estimated by spectrophotometry (Sartory and Groββelaar 1984; Wetzel and Likens 1991).

2.4.3 Winter ΔCO_2

The individual measurements of pCO_2 were converted to CO_2 concentration using Henry's Law and considering the water temperature. For each sampling date, we estimated the total CO_2 content of the lake by summing the CO_2 content of each one-meter stratum; the latter

was calculated as the product of the CO_2 concentration at that depth by the volume of the corresponding stratum (see description of bathymetric calculations below). CO_2 accumulation during winter was estimated as the difference in total lake CO_2 content between consecutive sampling dates (two to three) over the ice cover period. Because samples could not be taken for security reasons at the onset of the ice cover and prior to ice melt, accumulation rates over the entire ice cover period were extrapolated assuming that the rates determined over the central portion of the winter applied to either period (see Results section). The resulting values of total accumulation of either CO_2 are expressed in terms of total C per m^2 of lake, and are respectively referred to as areal winter CO_2 accumulation ($W\Delta CO_2$). Winter CO_2 accumulation is also expressed as a rate, in terms of C per unit of lake volume per day, calculated by dividing the total mass of C accumulated during winter ice cover period by the total lake volume; this is referred to as winter CO_2 accumulation rate ($W\tau\Delta CO_2$).

2.4.4 Summer hypolimnetic ΔCO_2

We used CO_2 profiles to determine the upper limit of the hypolimnion, because they offered a more relevant resolution than temperature alone. We fixed the upper limit of the hypolimnion as the depth under which pCO_2 increased during the summer stratification. In cases where this depth of the hypolimnion declined during summer stratification, we used the observed depth in the last summer sampling date for calculations of hypolimnetic volume and ΔCO_2. The sampling frequency did not allow us to determine exactly the onset of thermal stratification, especially in the boreal lakes. To derive a better estimate of the actual length of the stratified period we used the linear relationship between total CO_2 accumulation versus time to estimate the date that corresponded to a lake CO_2 content similar to that found at the end-of fall mixing CO_2 content, which is assumed to represent a mixing period steady state value. This assumption is supported by the low coefficient of variation (15%) of the total lake CO_2 content between the Fall of 2007 and the Spring/Summer 2008 samples, suggesting that when lakes are mixed for a certain period of time (15 to 30 days after complete mixing, during Spring or Fall), they tend to reach a steady state in terms of CO_2 content. This

hypothesis is further supported by the low coefficient of variation (12%) in the total lake CO_2 content between the open water samplings of the lakes that were never thermally stratified during summer (Lake 2, Lake 11 and EM-320). For some lakes, sampling coincided with the timing of fall overturn, so the end of the summer stratification was estimated using the actual field observations.

The hypolimnion was divided into 1-meter strata, and for each sampling date, we estimated the total CO_2 content of the hypolimnion by summing the CO_2 content of each stratum as described for the winter. The rate of CO_2 accumulation in the hypolimnion was calculated as the difference in total hypolimnetic CO_2 content between successive sampling dates, and as with the winter, accumulation rates over the entire stratified period were extrapolated assuming that the rates determined over the central portion of the summer applied to the entire stratification period. As with the winter, summer hypolimnetic CO_2 accumulation is expressed both in terms of total C per m^2 of lake ($H\Delta CO_2$) and as a rate, in terms of C per unit of lake volume per day, calculated by dividing the total mass of C accumulated during the stratification period by the total hypolimnetic volume; this is referred to as hypolimnetic CO_2 accumulation rate ($H\tau\Delta CO_2$).

On some occasions, the depth profiles were not carried out in the deepest portion of the lake, or the lake depth exceeded the length of the probe cable (Lake Bowker); in either case, there were strata that were not sampled for pCO_2, both for the winter and hypolimnion. In these cases, we assumed that the average volumetric rates of CO_2 accumulation that were estimated from the sampled depths of the hypolimnion also applied to the deeper strata that were not sampled; for these strata we then estimated the total CO_2 accumulation using the above rates and the corresponding volume, and added the resulting mass of C to that estimated for the sampled portion. The missing depths usually corresponded to less than 5% and 15% of the winter and hypolimnetic volume, respectively.

2.4.5 CO_2 fluxes

Gas exchanges at the air-water interface are a function of the concentration gradient between the water and the atmosphere, and the piston velocity of the gas. Piston velocity (k), which corresponds to the speed of exchange of a given gas at the air-water interface, is known to vary with temperature and wind speed, among others. To estimate the piston velocity for our lakes, we used the relationship by Cole and Caraco (1998), which is more adequate for relatively low wind environments (< 3 m s^{-1}) such as the ones we encountered (the mean wind speed during sampling in James Bay was 3 m s^{-1} and 2,2 m s^{-1} in the temperate regions):

$$k_{600}=2.07 + 0.215U_{10}^{1.7} (1)$$

where k_{600} is the piston velocity normalized for a Schmidt number of 600 at 20°C, U_{10} is the wind speed at 10 meters from the lake surface. For the temperate lakes, we used daily wind speed measured by the closest (less than 30 km from the sampling sites) meteorological stations available (Environnement Canada and Université de Montréal). For Boreal lakes, we measured the wind during summer using a Kestrel 3000 (Nielsen Kellerman Inc) anemometer at each sampling site for all dates and wind speeds was converted to U_{10} according to Amorocho and DeVries (1980). In order to estimate an open water mean k_{600}, we divided wind speeds in classes with an interval of 1 m s^{-1} and calculated the probability of each class to occur during the ice-free period for each of the Laurentians, the Eastern-Townships and the Boreal lakes, respectively. We then estimated an open water weighted average k_{600} for each region, which is pondered for the observed frequency distribution of wind speeds, using the following equation:

$$k_{600wa}=\Sigma[p_i \times k_{600i}] (2)$$

where k_{600wa} is the weighted average k_{600}, p_i is the probability of a wind speed in the class i to occur, and k_{600i} is the k_{600} for the wind speed class i (i=0 to 9 m s^{-1}). Regional piston velocities were than calculated for CO_2 for the surface water temperature of each sampling date using Jähne and others (1987):

$$k_{gas1}/k_{gas2}=(Sc_{gas1}/Sc_{gas2})^{1/2} (3)$$

where k_{gas} is the k_{600wa} described above, and Sc is the Schmidt numbers (Wanninkhof 1992) of the gas for the corresponding water temperature. The CO_2 flux was calculated for each sampling date as in Wanninkhof and others (1987):

$$\text{Flux} = \mu k \, (K_h \times [pCO_{2water} - pCO_{2air}]) \quad (4)$$

where μ is the chemical enhancement factor (see below), k is the weighted-average piston velocity from equation 3, K_h is the Henry's constant for CO_2 at a given temperature and salinity, pCO_{2water} is the partial pressure of CO_2 in the water measured at 0.5 meter depth, and pCO_{2air} is the partial pressure of CO_2 in the overlying atmosphere. In all cases, the surface pH was below 8 and in almost all cases the surface water was CO_2 supersaturated (exceptions: lake Connelly on three occasions and lake Bran de Scie on one occasion). Under these conditions, the chemical enhancement factor (μ) is negligible (Wanninkhof and Knox 1996).

2.4.6 Annual CO_2 fluxes and contribution of winter and hypolimnion

To estimate the net annual CO_2 emission, we integrated the fluxes calculated from measured surface pCO_2. For temperate lakes, monthly measurements of pCO_2 (from May to October) were available including spring and fall mixing periods. In the case of boreal lakes, we only sampled from June to September. To account for the lack of actual pCO_2 measurements in the weeks immediately after ice melt in the boreal lakes, we assumed that the accumulated CO_2 under the ice was entirely emitted from the system over a 1-month period after ice melt (Huotari and others 2009) and that these fluxes coming from winter accumulation were superimposed to a spring baseline flux value. We further assumed that the baseline spring CO_2 flux was similar to that observed in late spring (June). The relative contribution of winter and summer hypolimnion was calculated as the ratio of winter or hypolimnetic ΔCO_2 to the open water net CO_2 fluxes.

2.4.7 Bathymetry

The bathymetric survey was carried out in the context of a parallel study that focused on sediment C stocks in these same lakes (Ferland, in prep). The lake bathymetry was determined by ecosounding using a sub-bottom profiler (Bathymetric Survey System BSS+3 depth sounder, Specialty Devices Inc) connected to a GPS. The instrument was towed on a boat following a zigzag pattern across the surface of the entire lake; the resulting transects were used to reconstruct the three-dimensional shape of the entire lake basin, using ArcGIS (v9, ESRI Inc) software to extrapolate the depth measurements; total lake volume, and the surface and volume of each 1-m stratum were then calculated also using ArcGIS software.

2.4.8 Statistical analyses

Statistical analyses were performed using the platform JMP v7.0 (SAS Institute Inc). We used standard least squares regressions and data was log-transformed to attain normality and homoscedasticity. We used a probability threshold of 0.05 for statistical significance. Data points with studentized residuals exceeding three were excluded from the regressions. All means are presented with their standard deviation.

2.5 RESULTS

2.5.1 General lake characteristics

Basic limnological data of the studied lakes are summarized in Table 2.1. Mean summer TP ranged from 5.6 to 17.2 μg L^{-1}, mean DOC concentration ranged from 2.5 to 11.4 mg L^{-1} and the boreal and temperate lakes did not differ in average TP but differed in terms of their mean DOC concentrations (mean ± standard deviation: 7.6 ± 1.9 and 4.5 ± 1.5 mg L^{-1}, respectively; Wilcoxon; $n_1 = 12$; $n_2 = 4$; $p = 0.01$). Secchi depth was strongly negatively correlated to DOC (Pearson; $r = -0.91$; $p < 0.0001$), suggesting a major role of DOC in determining the light climate in these lakes. TP, DOC, secchi and mean depth were strongly correlated to each other (Pearson; $r > |0.6|$; $p < 0.005$), i.e. lakes that had low mean depth tended to have low secchi and higher DOC and TP concentrations. The lake area to catchment area ratio was correlated to TP (Pearson; $r = -0.7$; $p < 0.005$), and DOC (Pearson; $r = -0.6$; $p = 0.02$; Lake Connelly and Bran de Scie excluded).

Table 2.1 General characteristics of the studied lakes (CA = catchement area, LA = Lake area, $\bar{Z}$ = mean depth, TP = total phosphorus and DOC = dissolved organic carbon), total annual CO_2 fluxes estimated from surface pCO_2 (positive values are emissions), total areal winter ($W\Delta CO_2$) and hypolimnetic ($H\Delta CO_2$) CO_2 accumulation with (in parentheses) their respective contribution to net annual CO_2 emissions (WRC and HRC, in %) and volumetric rates of CO_2 accumulation during winter ($W\tau\Delta CO_2$) and in the hypolimnion ($H\tau\Delta CO_2$).

Lake	Location	**CA** km^2	**LA** km^2	**$\bar{Z}$** M	**TP** $\mu g\ L^{-1}$	**DOC** $mg\ L^{-1}$	**CO_2 fluxes** $g\ C\ m^{-2}\ yr^{-1}$	**$W\Delta CO_2$ (WRC)** $g\ C\ m^{-2}$	**$H\Delta CO_2$ (HRC)** $g\ C\ m^{-2}$	**$W\tau\Delta CO_2$** $mg\ C\ m^{-3}\ d^{-1}$	**$H\tau\Delta CO_2$** $mg\ C\ m^{-3}\ d^{-1}$
Bowker	45°24'N, 72°13'W	10.9	2.45	23.6	5.6	2.5	26.3	10.1 (38.4)	5.23 (19.9)	3.53	2.14
Croche	45°59'N, 74°00'W	0.89	0.19	4.9	5.6	4.7	44.5	10.3 (23.2)	1.67 (3.8)	15.4	15.1
Connelly	45°53'N, 73°57'W	24.4	1.24	7.7	9.8	4.4	25.3	13.9 (54.9)	11.0 (43.4)	13.3	22.4
Bran de Scie	45°24'N, 72°12'W	26.3	0.13	3.2	17.2	6.2	77.8	5.22 (6.7)	3.75 (4.8)	12.1	37.3
Natel	52°11'N, 75°40'W	17.1	3.79	5.4	6.2	6.4	36.3	11.2 (30.8)	1.70 (4.7)	11.3	20.3
Lake 60	52°13'N, 75°45'W	9.34	1.35	5.7	6.3	6.0	27.9	7.28 (26.0)	2.08 (7.4)	6.96	15.4
Labyrinthe	52°13'N, 75°42'W	10.5	1.55	4.5	7.2	9.6	43.6	8.61 (19.8)	3.89 (8.9)	10.4	24.5
Lake 34	52°58'N, 75°46'W	4.33	0.45	4.5	8.1	8.5	32.4	7.54 (23.3)	1.88 (5.8)	9.13	23.2
Lake 8	52°07'N, 75°43'W	2.80	0.30	2.6	8.3	6.4	32.8	6.29 (19.2)	0.26 (0.8)	13.3	12.4
Brendan	52°03'N, 75°30'W	3.56	1.04	3.8	8.5	5.5	29.6	8.32 (28.1)	1.39 (4.7)	11.9	12.6
Lake 40	52°01'N, 75°31'W	1.86	0.16	4.5	9.0	5.2	40.0	9.80 (24.5)	2.40 (6.0)	11.9	15.9
Mistumis	52°09'N, 76°09'W	19.1	3.85	2.1	9.1	7.6	31.5	3.95 (12.5)	0.48 (1.5)	10.4	15.1
EM-320	52°09'N, 76°07'W	4.54	0.45	2.4	9.6	7.8	55.0	5.54 (10.1)	-	12.9	-
Lake 11	52°08'N, 75°45'W	2.51	0.36	1.6	10.2	9.7	49.9	7.31 (14.7)	-	24.5	-
Lake 2	52°07'N, 75°49'W	2.26	0.04	1.5	11.4	11.4	46.4	15.9 (34.3)	-	57.9	-
Lake 66	52°57'N, 76°00'W	0.92	0.07	4.1	11.5	9.0	55.9	9.76 17.4)	5.01 (9.0)	13.2	39.4

2.5.2 Winter conditions

Ice cover length was 182 ± 15 days (Nov 15th, 2007 to May 15 2008) for the boreal lakes, and 136 ± 15 days (Dec 1st, 2007 to April 15, 2008) for temperate lakes, except for lake Bowker, which was covered by ice for 121 ± 15 days (December 15, 2007 to April 15, 2008). The thickness of the ice varied from 30 to 100 cm, and during the sampling period, there were on average more than 20 cm of snow overlying the ice. Under-ice PAR measurements showed that less than 1% of the incident light reached the water layer below the ice at least during the periods sampled. Typical winter temperature profiles were observed: Temperature was near 0°C under the ice, with a sharp increase within the first meters (at a rate of 1.25°C m^{-1}), and a more gradual increase thereafter (at a rate of 0.05 to 0.10°C m^{-1}), reaching a temperature of approximately 4°C near the sediments. The winter volume-weighted mean temperature ranged between lakes from 1.2 to 3.0 °C (mean = 2.2 ± 0.6 °C).

2.5.3 Winter CO_2 dynamics

Figure 2.2A shows an example (from Lake Connelly) of a temporal succession of winter, under-ice pCO_2 profiles; all these profiles typically show a gradual increase with depth, and a more rapid increase towards the sediment. Lakes were consistently CO_2 supersaturated on all winter sampling dates, at all depths sampled. Under-ice pCO_2 varied from 500 to a maximum exceeding 7000 µatm in layers close to the sediment. Total winter CO_2 accumulation ($W\Delta CO_2$) varied from 4.0 to 13.9 g C m^{-2} (Table 2.1), with an overall mean of 8.3 ± 2.6 g C m^{-2}. The mean total $W\Delta CO_2$ for Boreal lakes (7.8 ± 2.1 g C m^{-2}) was slightly lower than for temperate lakes (9.9 ± 3.6 g C m^{-2}), but the two regions were not significantly different from each other (Wilcoxon; p = 0.2). Lake EM-320, Lake 34 and Lake 66 were only sampled in March due to dangerous flying conditions for the helicopters in December. To estimate $W\Delta CO_2$ for these lakes, we assumed that the winter CO_2 content at the time of ice formation was the same as in the fall overturn period (see Methods, Hypolimnetic ΔCO_2 for more details on this assumption). $W\Delta CO_2$ was positively related to mean depth (Figure

2.4A; Table 2.2, Equation 1), and the lakes from the two regions fit in the same relationship; $W\Delta CO_2$ was also related to maximum depth ($r^2 = 0.37$; $n = 14$; $p = 0.0481$; data not shown). $W\Delta CO_2$ was not related to any of the other variables tested (TP, DOC, Secchi, Chl *a*, lake volume, lake area or drainage ratio).

Volumetric rates of CO_2 accumulation in the winter ($W\tau\Delta CO_2$) varied from 3.5 to 24.5 mg C m^{-3} d^{-1} (Table 2.1) with an overall mean rate of 12.0 ± 4.5 mg C m^{-3} d^{-1}. $W\tau\Delta CO_2$ averaged 12.4 ± 4.5 mg C m^{-3} d^{-1} in boreal lakes, and 11.1 ± 5.2 mg C m^{-3} d^{-1} in temperate lakes, and did not differ significantly between regions (Wilcoxon; $p = 0.5$) but lakes Bowker and 11 were clear outliers within their respective regions, and when excluded, the mean temperate $W\tau\Delta CO_2$ tended to be higher than that of boreal lakes (Wilcoxon; $p = 0.06$). $W\tau\Delta CO_2$ was negatively related to mean depth (Figure 2.4B; Table 2.2, Equation 2) and showed a positive trend with TP (not significant). $W\tau\Delta CO_2$ was not related to maximum depth, water volume, lake area, DOC, Secchi or chlorophyll *a*.

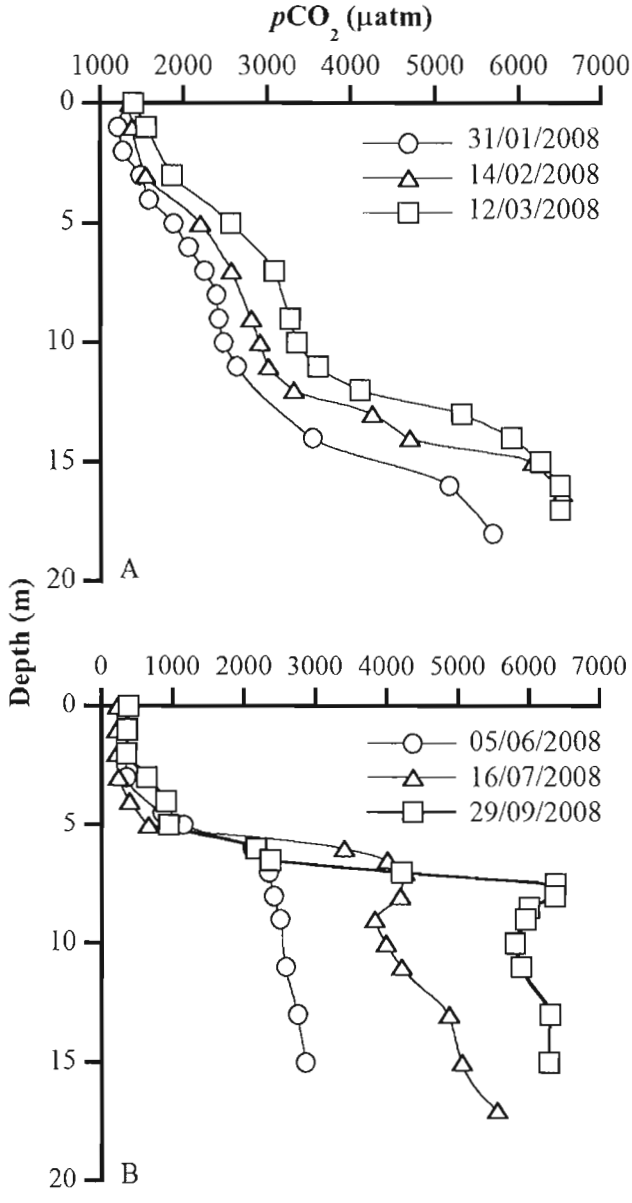

Figure 2.2 Succession of winter (A) and summer (B) pCO_2 profiles for Lake Connelly.

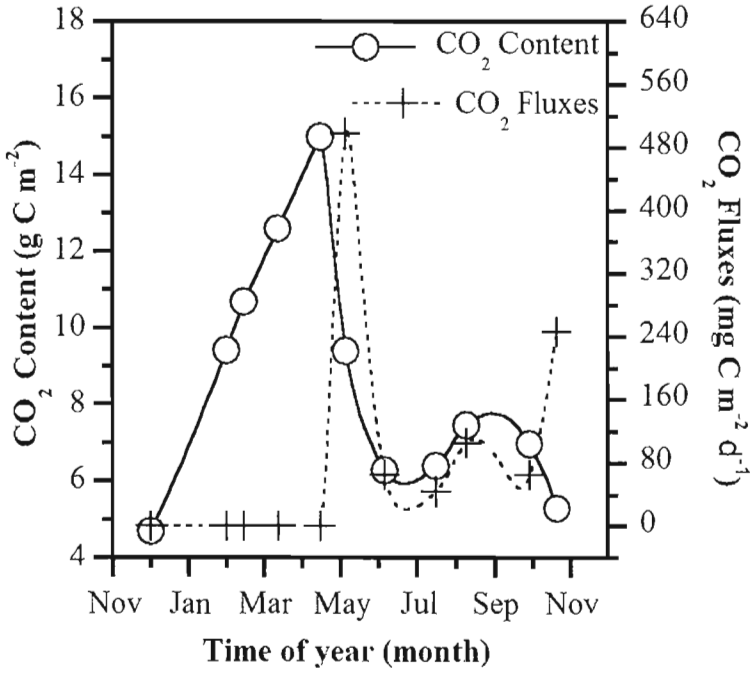

Figure 2.3 Annual cycle (from Nov. 2007 to Nov. 2008) of Lake Croche showing the increase of total CO_2 content under the ice and during summer stratification (solid line). The dashed line shows the daily fluxes estimated from pCO_2 measurements. The large declines in the CO_2 content during spring and fall mixing periods are associated with high emissions of CO_2 to the atmosphere.

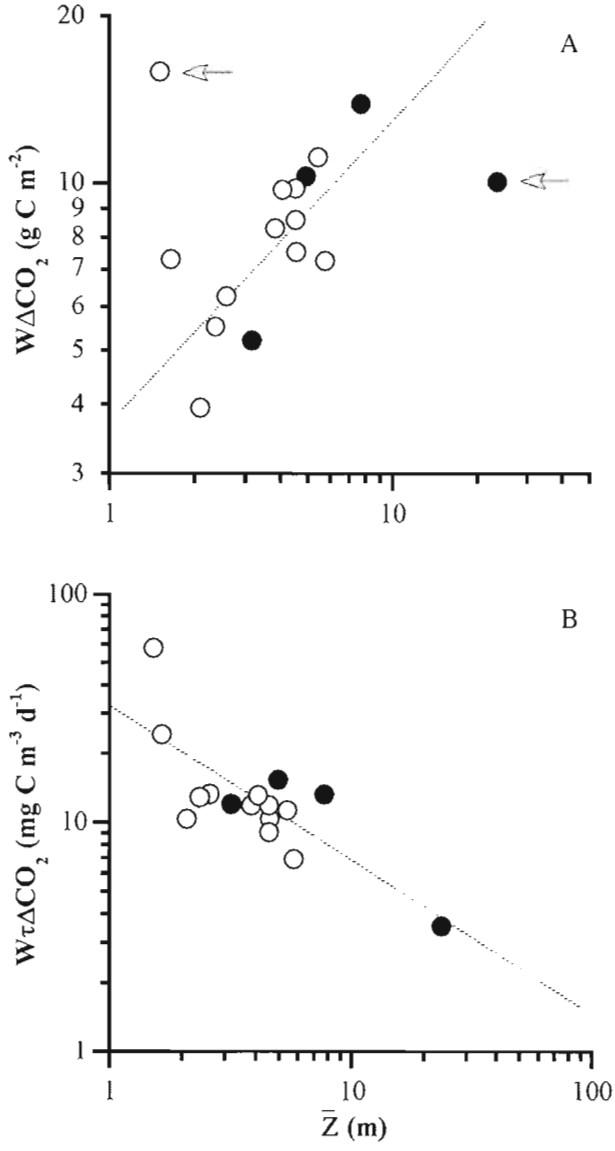

Figure 2.4 The relationship between winter areal CO_2 accumulation ($W\Delta CO_2$) and mean lake depth ($\bar{Z}$, panel A), and the relationship between winter volumetric CO_2 accumulation rates ($W\tau\Delta CO_2$) and mean depth (B). Outliers are marked with an arrow, and regression equations are in Table 2.2 (Equations 1 and 2). Open circles = Boreal lakes, Dark circles = Temperate lakes.

Table 2.2 Summary of the regressions (log-y = a * log-x+b). Significance of regression, r^2 and sample size (n) are shown. All data were log-transformed. The exclusion column lists outliers that were dropped from the regression model.

Equation	y	X	a	B	Prob.	r^2	n	Exclusion
1	$W\Delta CO_2$ (g C m^{-2})	$\bar{Z}$ (m)	1.28	0.59	< 0.0001	0.58	14	Bowker, Lake 2
2	$W\tau\Delta CO_2$ (mg C m^{-3} d^{-1})	$\bar{Z}$ (m)	-0.68	3.45	0.0003	0.61	16	
3	$H\Delta CO_2$ (g C m^{-2})	TP (µg L^{-1})	1.91	-5.7	0.0040	0.67	13	
		$\bar{Z}$ (m)	1.55					
4	$H\tau\Delta CO_2$ (mg C m^{-3} d^{-1})	TP (µg L^{-1})	1.39	-0.14	0.0274	0.37	13	
5	Annual CO_2 fluxes (g C m^{-2} yr^{-1})	DOC (mg L^{-1})	0.43	2.80	0.0114	0.40	15	Bran de Scie
6	Annual CO_2 fluxes (g C m^{-2} yr^{-1})	LA (km^2)	-0.15	3.57	0.0069	0.42	16	
7	WRC (%)	TP (µg L^{-1})	-1.28	5.67	0.0003	0.69	14	Connelly, Lake 2
8	HRC (%)	$\bar{Z}$ (m)	9.2	-19.3	0.0072	0.93	11	Connelly, Bowker
9	HRC (%)	$\bar{Z}$ (m)	2.70	-19.3	<0.0001	0.87	12	Bowker
		TP (µg L^{-1})	1.45	-5.32				

2.5.4 Hypolimetic conditions

Summer thermal stratification lasted on average 98 days (range: 73 to 101 days) for boreal lakes, and 145 days (124 to 187 days) for temperate lakes. Hypolimnetic volume corresponded to an overall mean of 31% (11 to 55 %) of the total lake volume. The volume-weighted hypolimnetic mean temperature ranged from 6.9 to 14.6 °C (mean: 11.7 ± 2.7 °C). The mean, volume-weighted hypolimnetic temperatures were significantly different between the two regions (Wilcoxon; p = 0.0055), boreal lakes having higher temperature in the hypolimnion (1.6 times higher, in average).

2.5.5 Hypolimnetic CO_2 dynamics

The total hypolimnetic CO_2 accumulation ($H\Delta CO_2$, expressed in g C m^{-2} of lake area) ranged from 0.3 to 11.0 g C m^{-2} (Table 2.1) with an overall mean of 3.1 ± 2.8 g C m^{-2}. The mean $H\Delta CO_2$ differed between the two regions (2.1 ± 1.5 g C m^{-2} and 5.4 ± 4.0 g C m^{-2} for boreal and temperate lakes, respectively), but the differences were not significant (Wilcoxon; p = 0.1). A stepwise regression including nutrients, temperature and morphometric variables retained only mean depth (positively related, Figure 2.5A) and TP (positively related), and boreal and temperate lakes followed the same relationship (Equation 3, Table 2.2). $H\Delta CO_2$ was not significantly related to lake area, lake volume or to the catchment area to lake area ratio.

Volumetric rates of CO_2 accumulation in the hypolimnion ($H\tau\Delta CO_2$) ranged from 2.1 to 39.4 mg C m^{-3} d^{-1} (Table 2.1), with an overall mean of 19.7 ± 10.1 mg C m^{-3} d^{-1}. $H\tau\Delta CO_2$ did not differ (Wilcoxon; p = 0.9) between boreal (mean = 19.9 ± 8.5 mg C m^{-3} d^{-1}) and temperate lakes (mean = 19.3 ± 14.7 mg C m^{-3} d^{-1}). The best predictor of $H\tau\Delta CO_2$ was TP (Figure 2.5B; Table 2.2, Equation 4). $H\tau\Delta CO_2$ was not related to morphometric variables or DOC. $H\tau\Delta CO_2$ was on average 1.8 times higher than $W\tau\Delta CO_2$ for the same lakes (Table 2.1), and both rates were not significantly correlated to each other (Figure 2.6). This suggests that there is not a close coupling between winter, under-ice and summer hypolimnetic processes.

2.5.6 Annual CO_2 fluxes

CO_2 fluxes (negative values are for influxes) to the atmosphere ranged from -10.5 to 757 mg C m^{-2} d^{-1}, and followed a similar seasonal pattern across lakes. Figure 2.3 shows a typical seasonal progression of CO_2 fluxes, determined for Lake Croche. Fluxes tended to be high in spring and in fall overturn (Figure 2.3), and lowest in the summer. On an annual basis, all lakes were a net source of CO_2 to the atmosphere, annual emissions ranging from 25.3 to 77.8 g C m^{-2} yr^{-1} (Table 2.1), with a mean of 40.9 ± 14 g C m^{-2} yr^{-1}. Net annual CO_2 fluxes were positively related to DOC (Figure 2.7A; Table 2.2, Equation 5), and negatively related to lake area (Figure 2.7B; Table 2.2, Equation 6).

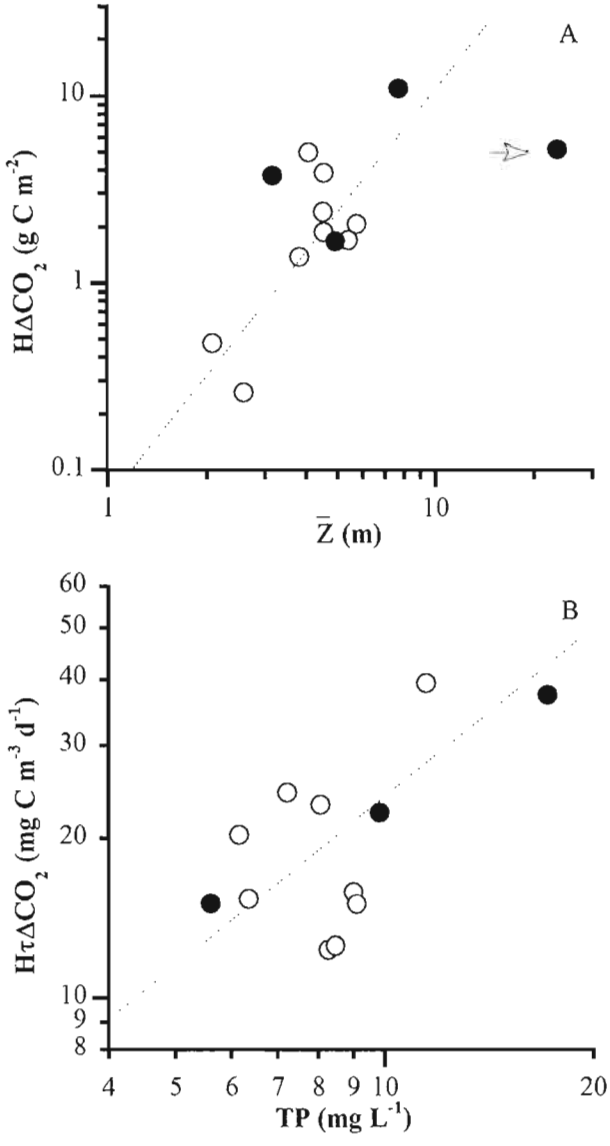

Figure 2.5 The relationship between (A) areal hypolimentic CO_2 accumulation ($H\Delta CO_2$) and mean depth ($\bar{Z}$), and (B) the relationship between volumetric CO_2 accumulation rates in the hypolimnion ($H\tau\Delta CO_2$) and total phosphorus (TP). The outlier is marked with an arrow. The regression equations are in Table 2.2 (Equations 3 and 4). Open circles = Boreal lakes, Dark circles = Temperate lakes.

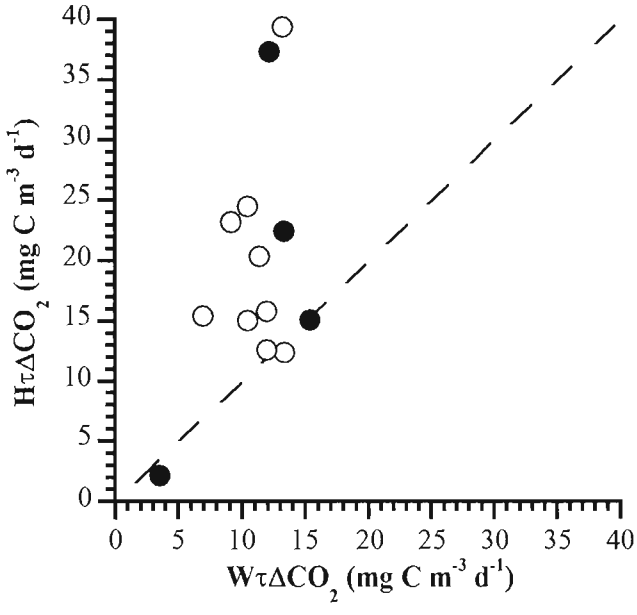

Figure 2.6 The relationship between volumetric hypolimnetic CO_2 accumulation rates ($H\tau\Delta CO_2$) and volumetric winter CO_2 accumulation rates ($W\tau\Delta CO_2$). Note the decoupling between winter and hypolimnion, and the larger range of variation of $H\tau\Delta CO_2$ relative to $W\tau\Delta CO_2$. The dashed line shows the 1:1 slope. Open circles = Boreal lakes, Dark circles = Temperate lakes.

2.5.7 Winter and hypolimnetic contribution to the annual CO_2 emissions.

The relative contribution of winter CO_2 accumulation to the net annual CO_2 emissions (WRC) ranged from 6.7 to 54.9 %. (Table 2.1), and was not significantly different between the two regions (Wilcoxon; $p = 0.7$). The overall average WRC was 24.0 ± 11.9%, and tended to decrease with increasing mean lake TP (Figure 2.8A; Table 2.2, Equation 7) and to increase with increasing DOC, although this relationship was not significant.

The relative contribution of hypolimnetic CO_2 accumulation to the net annual CO_2 emissions (HRC) ranged from 0.8 to 43.9 % (mean = 9.3 ± 11.3 %) (Table 2.1), and boreal lakes tended to have a lower HRC compared to temperate lakes (not significant). HRC increased with mean depth (Figure 2.8B; Table 2.2, Equation 8). A stepwise regression including all nutrients and morphometric variables, retained only TP (positively related) and mean depth (positively related) in the model (Table 2.2, Equation 9).

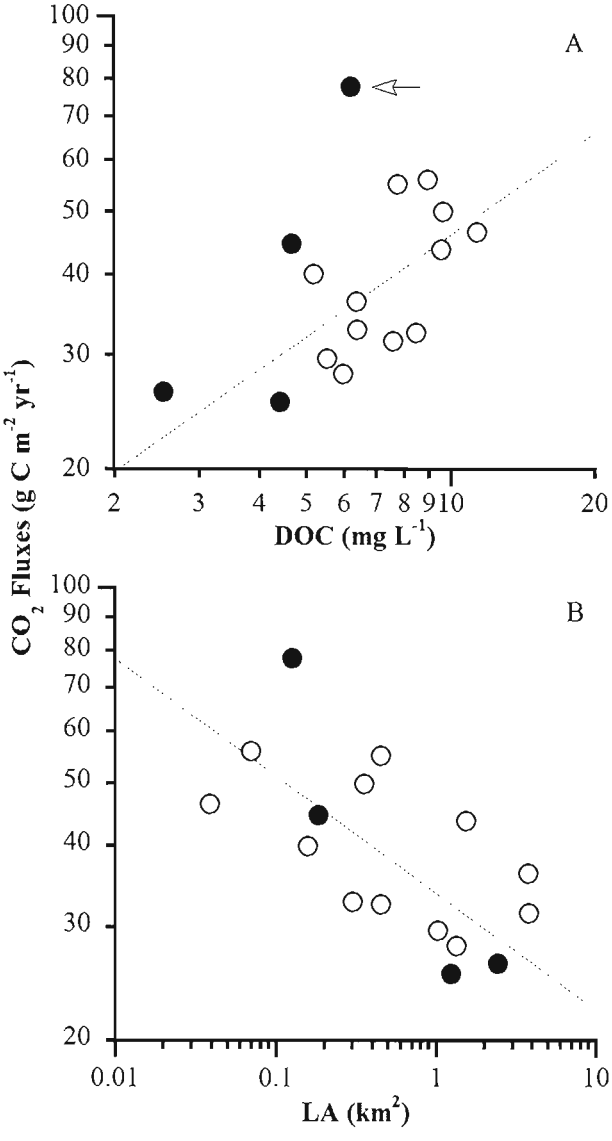

Figure 2.7 Relationships between net annual CO_2 emissions and dissolved organic carbon (DOC, panel A) or lake area (LA, panel B). Outliers are marked with an arrow, and the regression equations are in Table 2.2 (Equations 5 and 6). Open circles = Boreal lakes, Dark circles = Temperate lakes.

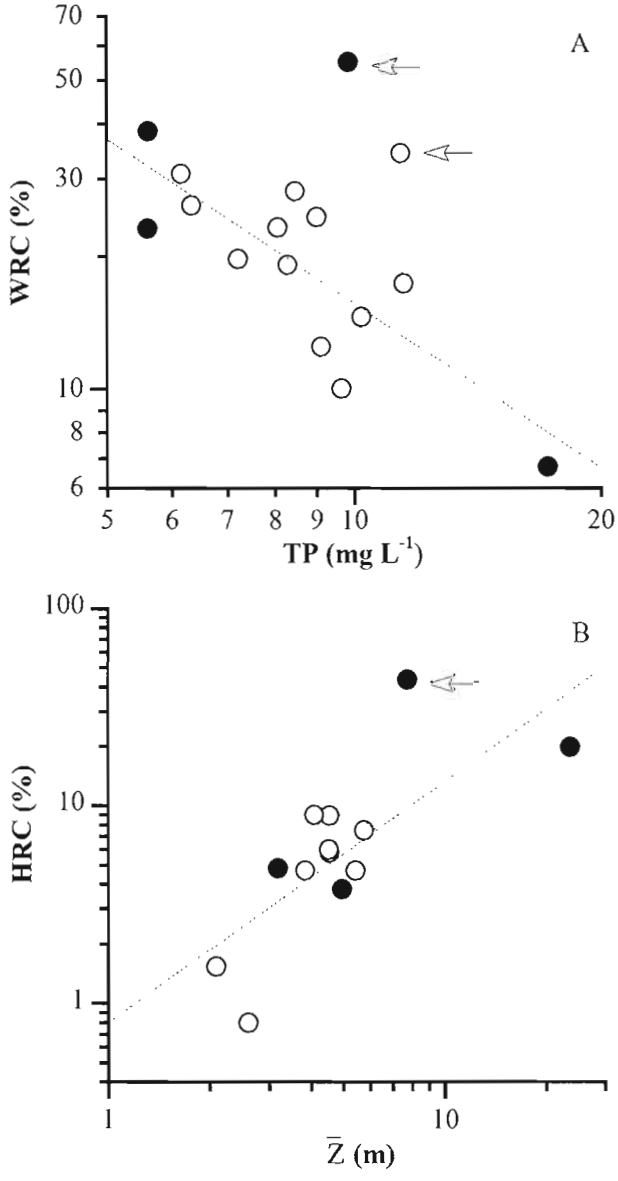

Figure 2.8 The contribution of winter CO_2 accumulation to the annual net CO_2 emissions (WRC) as a function of TP (A), and (B) the contribution of hypolimnetic CO_2 accumulation to annual net CO_2 emissions (HRC) as a function of mean depth ($\bar{Z}$). Outliers are marked with an arrow, and the regression equations are in Table 2.2 (Equations 7 and 8). Open circles = Boreal lakes, Dark circles = Temperate lakes.

2.6 DISCUSSION

2.6.1 Methodological uncertainties

There are several assumptions or processes that may influence our results. Two to three weeks before ice melt, thinner ice conditions and loss of snow cover may allow significant rates of primary production. For safety reasons, we did not sample during this period, rather we assumed that CO_2 accumulation rates were the same as measured during the winter; this could result in a slight overestimation of $W\Delta CO_2$, which based on previous studies, should not exceed 5 to 10% (Huotari and others 2009). For several lakes we could not have full CO_2 profiles to the bottom, and had to assume that rates of CO_2 accumulation observed in the upper layers of the hypolimnion and ice-covered lakes applied to the missing depths in the bottom of the lake. Since rates of CO_2 accumulation usually increase towards the sediments during both winter ice-cover and summer stratification, this assumption may result in a slight underestimation of the overall rate of CO_2 accumulation, especially when missing depths represented a large proportion of the water volume (i.e. Lakes Bowker and Natel). During summer sampling, lakes were generally well stratified, but we cannot exclude that high wind conditions and drops in summer temperature, especially in the boreal region, could have resulted in partial mixing of the water column between sampling dates. Finally, sampling at the central point of lakes assumes of a complete horizontal mixing, and thus spatial heterogeneity (ex. more active littoral zones) is not taken into account.

2.6.2 Winter CO_2 dynamics

Most previous studies reporting winter metabolic rates (Table 2.3) have focused on oxygen depletion rates. To facilitate comparison with published data, we converted our rates of CO_2 accumulation to Winter Oxygen Deficit Rate (WODR; expressed in m^2 of lake area) using an RQ of 1, which was empirically determined for these same lakes (Ducharme-Riel et al. Submitted, see Chapter 3). As shown in Table 2.3, our results were well within the range previously reported by other studies (Table 2.3). Our lowest values of WODR (Lake

Mistumis, 57 mg m^{-2} d^{-1}) was lower than the lowest rates observed in other studies. As discussed previously, the volume of Lake Mistumis may have been slightly underestimated due to sampling difficulties.

Total CO_2 accumulation during winter was relatively invariant (variation coefficient of about 31%) considering the range of lake morphometry and water chemistry. Surprisingly, there was no major difference in total winter CO_2 accumulation between regions, in spite of major differences in the length of winter ice cover and watershed features. Winter CO_2 accumulation should be greater in the boreal region where the winter ice cover is on average 35% longer, yet temperate lakes tended to have higher rates of CO_2 accumulation compensating for a shorter ice cover period. Shorter ice-cover periods seem to be somehow offset by higher rates and hypotheses about the underlying compensatory mechanisms are discussed further. The positive relationship between mean depth and areal winter CO_2 accumulation ($W\Delta CO_2$; Figure 2.4) suggests a significant role of pelagic processes in the accumulation of CO_2 during winter, and this observation is in accordance with results obtained by previous studies (Welch and others 1976; Barica and Mathias 1979; Mathias and Barica 1980; Babin and Prepas 1985). The role of pelagic processes in winter CO_2 dynamics is investigated further in a companion paper (Ducharme-Riel and others, submitted, see Chapter 3), where we have also explored the sources of organic matter supporting winter metabolism.

The negative relationship between $W\tau\Delta CO_2$ and mean depth (Figure 2.4B) could suggest either a dilution of benthic CO_2 in an increasingly deep water column, or the fact that pelagic processes tend to be slower in deeper lakes. All winter pCO_2 profiles (example in Figure 2.2) showed peak of pCO_2 near sediment, indicating diffusion of CO_2 from the sediment layer that contributes significantly to the pelagic CO_2 accumulation (see also Rantakari and Kortelainen 2005). Mean depth could also partly act as a surrogate for lake trophy, but $W\tau\Delta CO_2$ varied only by 37%, despite a four-fold variation in TP.

Table 2.3 Summary of the literature survey on winter oxygen depletion rates (WODR) and areal hypolimnetic oxygen demand (AHOD). Our data (in bold) was converted to WORD and AHOD assuming a respiratory quotient of 1.

Trophic status	Type	OD (mg m^{-2} d^{-1})	Measure	Reference
Oligotrophic to Mesotrophic	Boreal and Temperate	**57 to 273**	WODR	This study
Oligotrophic	Arctic	120 to 320	WODR	Welch and Bergmann (1985) White et al. (2008)
Oligo-mesotrophic	Subarctic	202	WODR	Karlsson et al. (2008)
Oligotrophic to Mesotrophic	Temperate	80 to 390	WODR	Welch et al. (1976)
Mesotrophic	Temperate	512	WODR	Baehr and Degrandpre (2002)
Eutrophic	Prairie Lakes	220 to 420	WODR	Barica and Mathias (1979)
Artificially Eutrophied	Boreal	110 to 400	WODR	Schindler (1990)
Oligotrophic to Hypertrophic	Boreal	243 to 848	WODR	Babin and Prepas (1985)
Oligotrophic to Mesotrophic	Boreal and Temperate	**48 to 595**	AHOD	This study
Oligotrophic to Mesotrophic	Temperate	101 to 900	AHOD	Charlton (1980) Cornett and Rigler (1987) Molot et al. (1992) Nürnberg (1995)
Hypertrophic	Temperate	1080	AHOD	Matthews and Effler (2006)

2.6.3 Hypolimnetic processes

Likewise to winter metabolic studies, research on hypolimnetic metabolism has mostly focused on O_2 consumption (Table 2.3). Again we converted our CO_2 accumulation to areal hypolimnetic oxygen demand (AHOD; expressed per m^2 of hypolimnetic surface area), also assuming a RQ of 1 (Table 2.3). Our results are well within the range previously reported (Nürnberg 1995). Our lowest value of AHOD (Lake 8) was lower than the lowest rates observed in other studies and this is explained by the fact that this lake had an extremely low ratio of hypolimnetic volume to total lake volume.

We found a positive relationship between areal CO_2 accumulation in the hypolimnion ($H\Delta CO_2$) and mean depth (Figure 2.5A), similar to that described for $W\Delta CO_2$, which suggests that pelagic processes in the hypolimnion also contribute significantly to CO_2 accumulation. In contrast to $W\Delta CO_2$, TP explained a significant part of the variation in $H\Delta CO_2$ (Table 2.2, Equation 3), as previously observed by Cornett and Rigler (1980), and volumetric rates of CO_2 accumulation in the hypolimnion ($H\tau\Delta CO_2$) were also positively related to TP (Figure 2.5B). It would thus appear that hyplomnetic CO_2 dynamics are more tightly coupled to lake trophy than winter CO_2 dynamics, and this coupling may explain the stronger cross-lake variation in $H\Delta CO_2$ (variation coefficient = 69%) relative to winter (31%). Not surprisingly, $H\Delta CO_2$ is on average higher in temperate lakes than in boreal lakes, the latter having a shorter summer stratification period.

2.6.4 Links between winter and hypolimnetic CO_2 dynamics

We found that total winter CO_2 accumulation was on average greater than hypolimnetic CO_2 accumulation (Wilcoxon; $p < 0.0001$), this despite the significant higher volumetric rates of CO_2 accumulation in the hypolimnion compared to winter (Wilcoxon; $p = 0.0087$). The ice cover period was longer to the summer stratification in boreal lakes, but approximately of the same length in southern lakes, and when these are considered separately, total CO_2 accumulation during these two periods was not statistically different in temperate lakes. This

would suggest that higher $H\tau\Delta CO_2$ compensates for the smaller water volume in the hypolimnion compared to under-ice water volume, but not high enough to compensate for major differences in the length of winter ice-cover relative to summer stratification.

The lack of relationship between $W\tau\Delta CO_2$ and $H\tau\Delta CO_2$ (Figure 2.6) has several implications. From a practical viewpoint, it suggests that it is not possible to predict winter CO_2 production rates on the basis of summer processes, and vice-versa. Conceptually, this lack of relationship suggests that the variables primarily regulating winter CO_2 accumulation may be different from those controlling these processes during summer, or alternatively, that these variables do not have the same influence on these two components of the annual cycle.

During summer, higher TP concentrations are associated with higher rates of primary production in lakes (Smith 1979) and higher metabolic rates in general (Ahrens and Peters 1991; Cimbleris 1998; Pace and Prairie 2005). Although primary production may not be significant in the hypolimnion itself, sinking of particulate organic matter from senescent algae of the upper strata (Baines and Pace 1994) results in inputs of freshly produced organic matter to the hypolimnion. Thus, it is not surprising that variations in lake trophy, here represented by a gradient in TP, should affect hypolimnetic CO_2 dynamics, influencing both areal and volumetric CO_2 accumulation rates in the hypolimnion. In contrast, trophic differences among lakes should be less apparent in winter, because differences in both microbial heterotrophs and benthic or planktonic autotrophs may be muted, the first being limited by low temperature and very low new inputs of organic matter (Felip and others 1996; Carlsson and Caron 2001), the second being limited by low, under-ice irradiance. This hypothesis is supported by the observed convergence in $W\tau\Delta CO_2$ in ice covered lakes that otherwise differ widely in lake trophy and morphometry. The apparent uncoupling between hypolimnetic and winter CO_2 dynamics does not imply that winter processes are completely disconnected from growing season features. There is probably a memory of summer productivity on winter processes, since CO_2 production during winter may rely partly on organic matter that was generated during the period of open waters (Karlsson and others 2008). This memory should be greater in lakes where the ice cover period is shorter, and this could explain why temperate lakes, which have a shorter ice cover period but similar ranges

of morphometric and nutrients variables, tend to have higher $W\tau\Delta CO_2$ compared to boreal lakes.

2.6.5 Contribution of winter and hypolimnetic CO_2 accumulation to annual C budgets

We found that both winter and hypolimnetic CO_2 production were significant components of the annual CO_2 budget of these lakes: Winter contributed between 7 to 55 % of the total annual net CO_2 fluxes while hypolimnion contributed from 1 to 44 % (Table 2.1). The CO_2 accumulated during both periods will eventually be fluxed to the atmosphere or exported via the outlet, yet it probably seldom accounted for in annual C budgets of lakes. For example, our more detailed sampling in the temperate lakes revealed that lake CO_2 content reached pre-ice values approximately 28 days (22 to 37 days) after the onset of ice-melt, suggesting that the CO_2 accumulated over the winter was completely released to the atmosphere within a few weeks, and due to concentration gradients, the bulk of emissions must occur within days of ice break. This period following ice-break in northern regions is typically undersampled, due to logistical and security issues, and thus the contribution of winter CO_2 production has probably been systematically underestimated in northern landscapes. Likewise, the bulk of hypolimnetic CO_2 accumulated during summer stratification will be released to the atmosphere within the two to three weeks following fall overturn (Figure 2.3), and will not be effectively captured unless the systems are followed closely in time. According to our results, ignoring winter and hypolimnetic contribution can lead to an average underestimation of 33 % of the net annual CO_2 emissions.

One of the consequences of the relatively narrow range of $W\Delta CO_2$ is that despite the wide range in lake area (0.04 to 4 km^2), no relationship was found between $W\Delta CO_2$ and lake size and with region. The corollary is that an average value of winter CO_2 accumulation (in our study 8.3 ± 2.6 g C m^{-2}) can be applied to both temperate and boreal lakes of various sizes to account for winter-derived CO_2 fluxes when the period following the ice melt is not sampled, assuming that all this CO_2 produced during winter will eventually be all emitted to the atmosphere.

The hypolimnetic contribution to annual net CO_2 emissions (HRC) was positively related to mean depth, and this relationship is to be expected, since deeper lakes have both deeper hypolimnia and longer and more stable stratification, but it also suggests a significant role of water column processes in the accumulation of CO_2. We explore this role in more detail in a companion paper (Ducharme-Riel et al. Submitted, see Chapter 3). HRC also increased with lake trophy, and this might be the result of higher availability of nutrient and organic matter to fuel decomposition.

It is interesting to note that, contrary to HRC, the relative importance of winter CO_2 accumulation to the annual CO_2 budget (WRC) peaked at both ends of the productivity spectrum (in both the most oligotrophic lakes, and in most productive lakes. This should generate a U-shaped pattern of winter contribution as a function of trophic status, for example, as summer TP, in these lakes. This pattern was not very clear, in part because we have few lakes in this high productivity category, and TP may not be the best indicator of primary production. Our data shows an initial decline in the WRC versus TP relationship (Figure 2.8A), and this pattern is probably due to a dilution of the winter signal, which does not vary greatly among lakes, with an open water signal that increasingly contributes to the annual flux as summer lake metabolism increases due to higher TP and DOC. However, beyond a certain threshold in nutrient enrichment, primary production in the surface layers becomes the major component determining the open water CO_2 balance, to the point where there may be net CO_2 uptake by the system. Under these circumstances, both the hypolimnion and the winter ice-cover periods become much more important again in determining the net annual emissions, because both accumulate larger amounts of CO_2 relative to net summer fluxes and thus, when these components are considered, lakes become a net annual CO_2 source to the atmosphere. Connelly is perhaps the example of a lake having high rates of primary production during the open water period, as suggested by the net uptake of CO_2 during most of the summer (data not shown) and where almost the totality of CO_2 effluxes observed in this lake occurred during spring and fall as a result of winter and hypolimnetic CO_2 accumulation. In this regard, Lake Connelly would have been erroneously considered as a net sink for CO_2 if winter and fall mixing would not have been considered.

2.6.6 Effects of climate and land use changes on winter and hypolimnetic CO_2 production

Mean annual temperatures and precipitation in the boreal region of northern Quebec are predicted to increase over the next 100 years between 3 to 7°C, and from 12 to 31%, respectively (Christensen and others 2007). In terms of temperature, northern boreal regions will become more similar to present day temperate regions. The temperate lakes targeted in our study had higher rates of winter CO_2 accumulation than boreal lakes of roughly similar morphometry, but since the ice-cover period was shorter, total winter CO_2 accumulation was similar between lakes in the two regions. This finding suggests that winter C accumulation may not necessarily decline under scenarios of reduced winter ice coverage induced by climate change, but rather that there may be compensatory mechanisms, as discussed previously. In our study, temperate and boreal lakes had similar rates of hypolimnetic CO_2 accumulation but had significantly different total hypolimnetic CO_2 accumulation, resulting from longer stratification periods in temperate lakes. Climate warming will probably result in longer and stronger stratification, and the importance of the hypolimnion will likely increase; epilimnetic metabolism will also increase as a result of warmer temperature, and further influence hypolimnetic metabolism. Climate changes will also induce shifts in regional vegetation and soil characteristics, and most likely changes in nutrient and DOC loading to lakes that may alter the lake CO_2 dynamics. The lack of significant difference between the annual CO_2 budgets of boreal and temperate lakes suggests that these regional changes may not induce major shifts on the total annual CO_2 budget, but rather influence the relative importance of the components of this budget.

2.7 CONCLUSION

One of our main conclusions is that winter C accumulation is in fact remarkably invariable (31%) across lakes of very different types and regions, and this allows the application of an overall mean value to lakes in general, both in boreal and temperate landscapes. This is important as a tool to incorporate winter to annual lake C budgets. There appears to be little memory of lake trophy and open water processes on winter CO_2 accumulation, but hypolimnetic CO_2 accumulation is more strongly coupled to summer productivity. There is also a convergence in total annual C emissions (per m^2) between lakes that varied by 3 orders of magnitude in lake area, 6-fold in DOC and 4 fold in TP. Winter may play an important role in this compensation, acting as a buffer to the divergence that occurs during the open water season. Hypolimnetic CO_2 accummulation was more variable among lakes than under-ice accumulation, but still much less variable than surface processes reported in the literature for most of these lakes (for example, variation coefficient of 300% in summer planktonic respiration, see Marchand 2007); in this regard, hypolimnetic processes may also play a buffering role in terms of cross-lake variability. Winter processes, and to a lesser extent, summer hypolimnia, thus confer temporal stability to the annual CO_2 dynamics, and also lead to a relative convergence of total annual fluxes among lakes that are very different. This in turn, implies that the aquatic portion of the landscape, taken as a whole, is a more constant and stable source of C to the atmosphere, with consequences on the regional C dynamics and budgets.

3. ARTICLE II

WINTER AND HYPOLIMNETIC CO_2 ACCUMULATION IN BOREAL AND TEMPERATE LAKES: BENTHIC AND PELAGIC CONTRIBUTION, AND LINKS TO RESPIRATORY QUOTIENT AND SOURCES OF ORGANIC MATTER CONSUMED[1]

Ducharme-Riel, Véronique, Paul A. del Giorgio and Yves T. Prairie[2]

This paper is submitted to the journal *Limnology and Oceanography.*

Authors contributions:

VDR: Designed the study, sampling, analysed the data and wrote the paper.

PAdG: Conceived and designed the study, analysed the data and wrote the paper.

YTP: Designed the study, analysed the data and wrote the paper.

[1] All cited references are grouped in a single reference section at the end of the thesis.

[2] Département des Sciences Biologiques, Université du Québec à Montréal, Case Postale 8888, succursale Centre-Ville, Montréal, QC, H3C 3P8, Canada.

3.1 Acknowledgments

Thanks to Lisa Fauteux, Marie-Eve Ferland, François Guillemette, Pierre Marcoux, Martine Camiré, Annick St-Pierre, Jérôme Comte and Environnement Illimité for field support. We are grateful to Catherine Beauchemin and Alice Parks who helped with lab work. Thanks to Jean-François Hélie and Roxane Maranger for their advice during project planning. We are also thankful to Alain Tremblay of Hydro Québec for providing logistic support to carry out the field component. Financial support for this project came from the Eastmain-1 project funded by Hydro-Québec, from the Natural Sciences and Engineering Reasearch Council of Canada (NSERC), and by a graduate scholarship to VDR from the Quebec fund for natural sciences and technologies (FQRNT).

3.2 Abstract

Northern lakes are now recognized as important sites of both C storage and C emission to the atmosphere, and there is increasing interest in understanding the processes that modulates C dynamics in these systems. In northern boreal and temperate lakes, the winter ice-cover and the summer hypolimnion both accumulate significant amount of CO_2 that can contribute to over a third of the annual lake CO_2 budget. Therefore the processes generating CO_2 during the ice-cover period and in summer hypolimnia need to be better understood. Here we explored the contribution of biotic processes to CO_2 accumulation, the dynamics of pelagic community respiration, the contribution of benthic respiration, the sources of organic matter fuelling respiration and the ecosystem-level RQs during the ice cover period and in the summer hypolimnia of a set of four temperate and 12 boreal lakes of varying size and trophic status. CO_2 accumulation in these lakes was dominated by biological aerobic pathways. Pelagic respiration measured by O_2 consumption in dark incubations varied from 0.1 to 8.2 mg C m^{-3} d^{-1} during the winter ice-cover, from 0.2 to 71.4 mg C m^{-3} d^{-1} in the hypolimnion and from 6.2 to 204.7 mg C m^{-3} d^{-1} in the epilimnion, and seasonal variation in pelagic respiration rates was mainly modulated by water temperature. Benthic respiration, estimated by difference between total CO_2 accumulation and pelagic respiration, contributed in average to over half (59 to 74%) of the total CO_2 accumulation during the ice-cover period suggesting that benthic respiration play a key role in winter under-ice CO_2 accumulations. The isotopic signature in $\delta^{13}C$ of the organic matter consumed, obtained from the Keeling plot method, ranged from -34.5 to -28.8 ‰ in summer hypolimnia whereas they ranged from -28.2 to -21.5 during winter ice-cover. These values hints toward a clear seasonal shift in the relative importance of the different sources of organic carbon fuelling respiration, suggesting a key role of benthic algal primary production in supporting winter metabolism in many of these lakes and a more significant contribution of phytoplanktonic OC in fuelling hypolimnetic metabolism. The ecosystem-level RQs ranged from 0.41 and 1.51 for both winter ice-cover and summer hypolimnia, and they were linked to the sources of organic matter respired. Our study outline the importance of considering the origin of OC fuelling CO_2 production in lakes given that this can both shape lakes gas balance and determine their role as a net source or sink of C at regional scale.

Key words: lakes CO_2 accumulations, boreal, temperate, winter ice-cover, summer hypolimnia, annual cycle, pelagic community respiration, benthic respiration, sources of OC consumed, respiratory quotients.

3.3 Introduction

Northern lakes are generally supersaturated in CO_2 (Cole et al. 1994; Kling et al. 1991), and are therefore net sources of CO_2 to the atmosphere. Recent estimates suggest that lake C emissions may potentially be of similar magnitude as other better known components of the global C cycle, such as forest fires and river C inputs to the oceans (Cole et al. 2007; Tranvik et al. 2009), yet C fluxes from lakes to the atmosphere have seldom been considered in regional or global C budgets. Two of the main obstacles to the inclusion of lake processes in regional C models and budgets are 1) the paucity of complete annual lake emission budgets, and 2) the lack of models that allow to extrapolate these annual lake budgets to the ensemble of lakes in a region.

Regarding the former, most studies that have addressed CO_2 fluxes have focused on the surface waters of lakes during the open water season, and have generally ignored processes that occur during winter months, especially under the ice in high-latitude regions, and in deeper water layers during summer stratification. These sampling biases may potentially result in major errors in the estimated annual emission budget of lakes, particularly in lake-rich temperate and boreal landscapes where ice cover is present for over a third of the year (Striegl et al. 2001). Our own studies (Ducharme-Riel et al. submitted) have shown that in northern boreal and temperate lakes in Quebec, the period of winter ice cover, as well as the summer stratification, result in large CO_2 accumulations, which collectively contribute on average to over 30% of the net annual CO_2 emissions of these lakes. It is clear that winter and hypolimnetic C dynamics need to be better understood, in particular, in terms of both the processes that generate this CO_2, and the sources of C that fuel them.

CO_2 originates from the biological and abiotic decomposition of organic matter from aquatic and terrestrial origin (Granéli et al. 1996), from ground- and surface water inputs of DIC (Striegl and Michmerhuizen 1998), and from in-lake chemical processes. Lake morphometric, catchment and climate characteristics, which in turn shape the physical structure of lakes, as well as inputs of nutrients and organic matter to lakes, have all been linked to lake CO_2 accumulation and the resulting emissions to the atmosphere (Kortelainen

et al. 2006; Rantakari and Kortelainen 2005; Sobek et al. 2003). In lakes where CO_2 originates mostly from decomposition of organic matter, microbial respiration, and the variables that modulate microbial metabolism, such as the quality and the availability of nutrients and organic matter (Carlsson and Caron 2001; Cimbleris and Kalff 1998; Felip et al. 1996), play a key role in the CO_2 dynamics (Marchand 2007). Microbial metabolism is probably the dominant process underlying CO_2 accumulation during winter ice-cover and in the summer hypolimnion in many northern lakes, since photochemical production and groundwater CO_2 injection are probably at a minimum during those periods, but this hypothesis has seldom been tested.

Microbial metabolism can occur in both the water column and in the sediments, but the relative importance of these pathways during summer stratification and especially during winter ice-cover has not been well explored. Lake morphometry and trophic status also influence the relative importance of benthic versus pelagic processes in lake CO_2 dynamics (Kelly et al. 2001). Smaller and less productive lakes typically have a relatively greater contribution of the benthic compartment on C metabolism than larger or more productive lakes (Vadeboncoeur et al. 2008), and this probably applies to winter and hypolimnetic CO_2 production as well. For example, benthic metabolism accounts for a significant proportion of total hypolimnetic respiration (20 to 80%) in both small (Carignan and Lean 1991; Cornett and Rigler 1987; Linsey and Lasenby 1985) and large lakes (Jonsson et al. 2001). In this regard, Algesten et al. (2005) hypothesized that the contribution of sediments to total CO_2 production should be even more important during winter ice-cover, because pelagic CO_2 production is slowed down by low inputs of organic matter, the absence of photodegradation and by low temperatures. Sediments, being many-fold richer in nutrients and organic matter relative to the water column, and also adapted to consistently low temperatures (Pace and Prairie 2005), may sustain higher metabolic rates during winter periods. To our knowledge, only one study to date has actually quantified the relative contribution of benthic and pelagic metabolism to under-ice winter CO_2 build-up (Karlsson et al. 2008).

The processes that generate CO_2 in deep waters during summer stratification, and in winter under the ice cover, are strongly linked to the sources of organic C consumed to generate this

CO_2. There are two major sources of organic matter that can fuel biological CO_2 production in lakes (Kritzberg et al. 2004), i.e. organic carbon (OC) fixed within the lake (autochthonous OC) and organic carbon of terrestrial origin (allochthonous OC). There is increasing evidence that external inputs of organic carbon play a major role in shaping lake metabolism (Åberg et al. 2007; Karlsson et al. 2007; McCallister and del Giorgio 2008), and thus lake CO_2 dynamics (Marchand et al. 2009). In northern temperate and boreal lakes, the importance of these sources necessarily varies seasonally following changes in the loading and the relative availability of terrestrial versus algal organic matter. Little is known regarding seasonal shifts in the relative importance of the various sources of organic C in lakes, and particularly if the sources fuelling the biological production of CO_2 differ between winter ice cover (Karlsson et al. 2008) and summer stratification (Åberg et al. 2007; Houser et al. 2003).

The processes that generate lake CO_2, and the underlying sources of organic C, both in turn should influence the coupling between CO_2 and O_2 dynamics at the whole ecosystem level, particularly at times when either the entire lake, or a stratum within, are isolated from the atmosphere. Large deviations from physiological ranges of aerobic RQ (Williams and del Giorgio 2005) during the periods of isolation, i.e. the hypolimnion and the winter ice-cover, are evidence of the contribution of either anaerobic metabolic processes (Rich 1980), or abiotic processes that contribute to CO_2 disproportionately in regards to O_2. Thus the magnitude and variability of ecosystem-level RQ may provide further evidence for the pathways that lead to CO_2 accumulation during these periods.

In this paper, we explore CO_2 accumulation and C metabolism in both summer hypolimnia and under ice cover in a set of four temperate and 12 boreal lakes, located in three major regions of Québec. In particular, we studied the origin of the CO_2 that accumulates during these periods (abiotic versus biotic processes), the relative importance of pelagic versus benthic CO_2 production, the coupling between O_2 and CO_2 dynamics, i.e. the respiratory quotient at the ecosystem level, and the organic matter sources supporting biological CO_2 production during the two periods. The benthic contribution to total CO_2 accumulation in hypolimnia and winter ice-covered lakes was estimated by difference using measurements of pelagic respiration and total CO_2 accumulation rates. Ecosystem-level RQs were estimated on

the basis of departures from saturation along water column profiles during the two periods, to assess how the coupling between O_2 and CO_2 dynamics varied across lakes, and how it may be linked to the underlying processes and to the sources of organic matter consumed. Potential differences in the sources of organic matter consumed were determined from Keeling plots using the change in $\delta^{13}C$ isotopic signature of DIC during the ice cover period and summer stratification.

3.4 Methods

3.4.1 Study sites and sampling design

For this study we targeted a total of 16 lakes, within two broad regions (Figure 2.1). Four lakes were sampled in the southern temperate region of Québec: Two of these (Bowker and Bran de Scie) are located in the Appalachian area of Eastern-Townships, 150 km south of Montréal, and the other two (Croche and Connelly) are located in the Laurentian area of the Canadian Shield, 100 km North of Montréal; twelve lakes were further sampled in the Eastmain River region of boreal Québec, approximately 1500 km Northwest of Montréal. The two regions, boreal and temperate, are characterized by large differences in climate: Average January temperatures range from -30 to -15°C and from -20 to -5°C (Natural resources Canada, 2007B and C), respectively, and the length of lake ice cover is on average 180 and 140 days respectively (Ducharme-Riel et al. submitted). Average June temperatures in the boreal region range from 6 to 25 °C and from 11 to over 25 °C in the temperate region (Natural Resources Canada, 2007B and C). Lakes were selected within each region to obtain a range of nutrient concentrations and morphometry (Table 2.1), similar between the two regions.

3.4.2 Sampling

The four lakes in the temperate region were sampled monthly during an annual cycle, from Nov. 2007 to Nov. 2008. The twelve boreal lakes were also followed over an annual cycle but the sampling interval varied: They were sampled in June, July/August and September of both 2007 and 2008 (spring/summer samples), and in December 2007 and March 2008 (winter samples). Lakes were visited once during each sampling month, and sampled at their deepest and central point.

The percentage of incident light penetrating the ice cover (see chapter 2 for more details), as well as the light attenuation profile during open water period was determined with a Li-Cor

(Li-1400, quantum underwater cell 6574). Secchi depth was further measured for all lakes during the open water period. A detailed depth profile (one meter interval) of temperature, pH, conductivity, O_2, (using a YSI 600XLM, Yellow Spring Instruments Inc.), and pCO_2 was carried out at each sampling time. In situ pCO_2 was determined using an EGM-4 (PP Systems Inc.) connected to a gas equilibrator (Mini Module membrane contactor G542, Membrane Underlining Performance Inc.) in a closed recirculating loop and a peristaltic pump (Cole and Prairie 2009; Roehm et al. 2009). At the outlet of the peristaltic pump, a Y-shaped connection allowed the water to pass through the gas equilibrator for pCO_2 measurements or through a length of tubing to collect other types of samples at the desired depths. Water samples were collected at a 1 meter depth for total phosphorus (TP) and chlorophyll *a*. All tubes were acid washed and rinsed three times with nanopure and in situ water before filling.

3.4.3 Chemical analyses

Water for DOC and DIC was taken at 1 meter depth, middle water column and at 1 meter from the bottom during each winter sampling. Hypolimnetic DOC and DIC samples were taken at middle hypolimnion depth. Additional DIC samples were taken at the top and bottom of the hypolimnion of the temperate lakes for Keeling plots analyses (see below). Gas tight 40-ml vials were filled in situ with no bubbles for DIC. All DOC samples were taken in 60-ml syringes and water was then filtered with a 0.45 µm Sarstedt Filtropur capsule and poured into two 40-ml acid washed vials. Samples were kept colder than in situ temperature in their way to the lab to avoid further bubble formation and were stored at 3°C until analysis. DOC and DIC samples were passed through an O.I. Analytical 1010 TIC-TOC analyser within one week after sampling. TP was analysed with unfiltered samples after persulfate digestion, and chlorophyll *a* was extracted in ethanol and its concentration was estimated by spectrophotometry (Sartory and Groββelaar 1984; Wetzel and Likens 1991).

3.4.4 Changes in winter and hypolimnetic DOC and DIC concentrations

The changes in DOC concentration during winter ice cover (winter ΔDOC) were estimated by integrating the area under the curves of the DOC mass profiles. DOC mass is the product of the DOC concentration by the water volume of the corresponding one-meter stratum. The DOC mass of each one meter stratum was plotted as a function of depth of the strata. The integrated area of the last winter sampling was then subtracted from the area of the first winter sampling to obtain the total DOC change. For the summer stratification period, the DOC concentration was measured only at the mid-depth of the hypolimnion. Differences in concentration between consecutive sampling dates were used to estimate the average DOC change in the hypolimnion. In the lakes where isotopic analyses were conducted (see below), the changes in winter and hypolimnetic DIC concentration (ΔDIC) were also estimated using the same method as for ΔDOC. ΔDOC and ΔDIC are expressed as changes in DOC or DIC per unit volume (hypolimnetic volume or lake volume in winter, respectively) per day.

3.4.5 Winter and hypolimnetic ΔCO_2

Volumetric rates of CO_2 accumulation in the hypolimnion ($H\tau\Delta CO_2$) and in ice covered lakes ($W\tau\Delta CO_2$) were previously estimated in Ducharme-Riel et al. (submitted) and are presented in Table 2.1. The individual measurements of pCO_2 were converted to CO_2 concentration using Henry's Law. For each sampling date, we estimated the total CO_2 content of the ice covered lake and of the hypolimnion, respectively, by summing the CO_2 content of each one-meter stratum; the latter was calculated as the product of the CO_2 concentration at that depth by the volume of the corresponding stratum. CO_2 accumulation was estimated as the difference in total lake CO_2 content or total hypolimnetic CO_2 content between consecutive sampling dates (two to three) over the corresponding period. The resulting values of total accumulation of CO_2 are expressed in terms of C per unit of lake volume, or hypolimnetic volume per day calculated by dividing the total mass of C accumulated during winter ice

cover or summer hypolimnia by the total lake volume or the hypolimentic volume, respectively.

3.4.6 Isotopic analysis

The isotopic signatures in $\delta^{13}C$ of DIC and DOC were analysed during winter for all lakes and in the hypolimnion of the four temperate lakes during summer stratification. At each depth were DIC samples were taken, two additional gas-tight 40-ml vials were filled avoiding the formation of bubbles. Samples were then sent to G.G. Hatch Stable Isotope Laboratory (Ottawa) for $\delta^{13}C$ analysis of DOC and DIC where they were run in an O.I. Analytical Aurora 1030W TOC analyser connected to a mass spectrometer (Finnigan Mat DeltaAvantage). The isotopic signature is expressed relative to a standard using the notation δ in per mil (‰):

$$\delta^{13}C = (R_{sample} / R_{standard} - 1) \times 1000$$

where $R = {}^{13}C/{}^{12}C$ (Mckinney et al. 1950). Precision for isotopic determinations is ± 0.2 ‰.

3.4.7 Isotopic signature of the added DIC (Keeling plot method)

Respiration and other processes add DIC with a particular isotopic signature ($\delta^{13}C$) to the lake background DIC, and this added DIC accumulates during the ice cover period and in the hypolimnion. In cases where DIC accumulation during these periods is primarily due to respiration, the overall $\delta^{13}C$ signature of the added DIC will correspond to that of the sources of organic carbon respired. Organic carbon of different origins (terrestrial plant material, phytoplankton, benthic algae and macrophytes) has specific signatures in $\delta^{13}C$ (see Discussion and Figure 3.8). It is possible to estimate the isotopic signal of the added DIC using the Keeling plot method (Karlsson et al. 2007; Keeling 1958; Miyajima et al. 1997), which consists of plotting the $\delta^{13}C$ signature of the DIC that accumulates as a function of the inverse of the concentration of DIC; the intercept of this plot indicates the $\delta^{13}C$ signature of

the added DIC, the latter coming from the decomposition of a combination of different sources of organic carbon (when the added DIC has a metabolic origin). Keeling plot analyses were done for all lakes during winter, and for the four temperate lakes during summer stratification. DIC samples were not corrected for the proportion of DIC in the form of CO_2 because pH measurements were not available for winter due to a pH probe failure. We calculated the slope of the relationship between the rates of CO_2 accumulation and the rates of DIC accumulation to estimate the proportion of the added DIC that results from CO_2 accumulation during the winter ice-cover and in summer hypolimnia.

3.4.8 Pelagic Respiration

Pelagic respiration was estimated from changes in O_2 concentration versus time in short-term incubations in the dark, and O_2 concentration was measured using two different methods (see below). For all respiration experiments, water was taken at 1 meter depth under the ice (winter), 1 meter depth below the surface (open water period) and at middle hypolimnion. Due to logistical constraints, winter respiration was not measured in boreal lakes. In the lab, incubators were used to keep the incubation set ups (see below) at in situ temperature during the experiment. All incubation containers were acid washed and rinsed three times with nanopur and in situ water before use.

For temperate lakes, the method described in del Giorgio and Bouvier (2002) was used because it allows to measure low respiration rates in short incubations (< 24 hours). The incubation set-ups consisted of one 4-liter Erlenmeyer and a 4-liter flexible container (Cubitainer) connected via acid-washed tubing. The Erlenmeyer is used for the actual incubation and sampled through an exit port over the time course of the experiment, whereas the top container serves as a reservoir to replace the water sampled. These flow-through systems (one per site, per date) were incubated during 48 hours and were sampled every 6 to 8 hours by filling three seven-ml tubes that were then killed with a saturated solution of $HgCl_2$ and covered with a glass cap. Tubes were submersed in a water bath and kept at

incubation temperature prior to analysis. Samples were analysed within two weeks for oxygen concentration using membrane inlet mass spectrometry (MIMS, Kana et al. 1994).

The above method is difficult to use in remote areas because the MIMS is difficult to operate under such conditions, and the incubation systems require large temperature-controlled chambers or incubators. For respiration measurements in boreal lakes, O_2 concentrations were determined using optodes, with a Fibox 3 system consisting of an external fiber optic probe and oxygen mini-sensors fixed in the bottom of 500 ml Erlenmeyers, which were filled in situ and closed with a silicon cap (method detailed in Marchand 2007). The upper part of the Erlenmeyer is further covered with parafilm to ensure complete isolation. Measurements of oxygen concentration were made every 12 hours and water was incubated for a total of 60 hours. The oxygen mini-sensor allows to repeatedly measure oxygen concentration in the Erlenmeyers without exposing the samples to the atmosphere. The average error of O_2 measurements carried out this way is 8 $\mu g\ O_2\ L^{-1}$ (Marchand 2007).

The pelagic respiration rates (R) obtained by both methods were converted to carbon units assuming a RQ of 1. R is expressed as a volumetric rate of C production per day. In order to make cross seasonal comparisons, pelagic respiration rates were standardised at a temperature of 10°C (R_{std}) using the equation (6) between respiration and temperature provided by Pace and Prairie (2005), assuming a double logarithmic slope of 1.28, following Carignan et al. (2000).

3.4.9 Benthic contribution to total CO_2 accumulation

Benthic CO_2 production was initially estimated as the difference between total CO_2 accumulation rate (described above) and the mean pelagic respiration rate of the corresponding period (2 estimations per lake for winter; 2 to 4 estimations per lake for the hypolimnion). Since winter respiration rates were only measured for temperate lakes, an alternative method was also explored, based on ΔDOC as an approximation to pelagic CO_2 production.

The resulting benthic respiration rates (R_{bent}) derived from both methods are expressed in units of carbon per m^2 of sediment area per day. To allow cross seasonal comparisons, benthic respiration rates were also standardised to a temperature of 10°C using the equation provided in Pace and Prairie (2005), and a double logarithmic slope 0.65 for the relationship between benthic respiration and temperature (Pace and Prairie 2005). The benthic contribution to total CO_2 accumulation was estimated as the benthic respiration rate expressed volumetrically, i.e. in units of total lake volume for winter and of hypolimnetic volume for summer stratification, divided by the total winter or hypolimnetic CO_2 accumulation rate, respectively.

3.4.10 Ecosystem-level respiratory quotient (RQ)

RQs were estimated using orthogonal regressions of equal variance between the departure of CO_2 from saturation (Y) versus the departure of O_2 from saturation (X). CO_2 and O_2 at saturation were calculated using Henry's law. The last summer stratification profiles and the last winter profiles of CO_2 and O_2 were used to estimate the RQ of the hypolimnia and the ice-covered lakes, respectively.

3.4.11 Statistical analyses

Statistical analyses were performed using the platform JMP v7.0 (SAS Institute Inc). To study the patterns between the variables, we used standard least squares regressions and data were log-transformed to attain normality and homoscedasticity. We used a probability threshold of 0.05. Data points with studentized residuals superior to three were excluded from the regressions. Means are presented with standard deviation.

3.5 Results

3.5.1 General lake characteristics

Lake chemical and morphometric data are summarized in Table 2.1. Mean depth ranged from 1.5 to 23.6 m, and lake area ranged from 0.04 to 3.85 km^2. TP ranged from 4.0 to 17.2 $\mu g\ L^{-1}$ (mean ± S.D. 8.6 ± 2.8 $\mu g\ L^{-1}$). DOC ranged from 2.5 to 15.7 $mg\ L^{-1}$ (mean 7.1 ± 2.4 $mg\ L^{-1}$), and boreal lakes had significantly higher DOC concentrations than temperate lakes (Wilcoxon: $p = 0.01$). The percentage of incident light reaching the surface of the water column under the ice cover was below 1% during winter sampling. Incident light reaching the thermocline during summer stratification ranged from less than 1% to 6% in temperate lakes. Incident light under the thermocline was not measured in the boreal region but the colored nature of the water and the low secchi depth (0.9 to 3.2 m) suggest that the incident light reaching the hypolimnion of the boreal lakes was lower than in temperate lakes. Secchi depth was a function of DOC concentration (SLS; $r^2 = 0.89$; $n = 16$; $p < 0.0001$). DOC was significantly correlated to mean depth (Pairwise; $r = -0.81$; $p < 0.0001$; double log scale) and also to TP (Pairwise; $r = -0.59$; $p = 0.0160$; double log scale).

3.5.2 Winter and hypolimnetic oxygen dynamics

The studied lakes are mainly in the lower range of productivity and thus oxygen concentrations stayed well above 2 $mg\ L^{-1}$ for most of these lakes over the winter ice cover. However, hypoxic conditions (0.43 to 1.62 $mg\ O_2\ L^{-1}$) were observed immediately above the sediments in Lake Croche, Connelly and Bran de Scie throughout the winter period. Hypoxic conditions (0.21 to 1.79 $mg\ O^2\ L^{-1}$) were also recorded in the layer above sediment in Lakes Labyrinthe, 40, 66, 11 and 2, but only at the end of the winter. Likewise, we recoded hypoxia near the sediments in the hypolimnia of Lakes Bran de Scie, Croche and Connelly by mid august (0.01 to 0.83 $mg\ O_2\ L^{-1}$), and almost the entire hypolimnion of these lakes became hypoxic for the remainder of the stratification period (from late August to early October). In

the boreal region, only Lake 8 had hypoxic conditions above sediment during the last summer stratification sampling.

3.5.3 Pelagic respiration

The majority of the experiments showed a linear decrease of O_2 during the entire course of the incubation (48 to 60 hours), irrespective of the method used. Less than half of the time courses had erratic patterns of O_2 and were excluded from the analysis and, most of these erratic patterns were found in the hypolimnia when using the fibox method. Whenever possible, we used the data points of the first 24 to 48 hours of incubation to estimate pelagic respiration rates (R) because shorter incubations represent better in situ conditions (Gattuso et al. 2002).

Mean respiration rates for the winter and the hypolimnion are presented in Table 3.1. Considering all seasons and sites, pelagic respiration (R) ranged from 0.1 to 204.7 mg C m^{-3} d^{-1}. Winter R (data available for temperate lakes only) ranged from 0.1 to 8.2 with an overall mean of 3.1 ± 1.0 mg C m^{-3} d^{-1}. Summer epilimnetic R ranged from 22.3 to 107.8 mg C m^{-3} d^{-1} (mean 42.5 ± 19.0 mg C m^{-3} d^{-1}) for boreal lakes, and from 6.2 to 204.7 (mean 63.7 ± 52.3 mg C m^{-3} d^{-1}) for temperate lakes. In boreal lakes, hypolimnetic R ranged from 1.4 to 17.9 mg C m^{-3} d^{-1} (mean 6.3 ± 5.5 mg C m^{-3} d^{-1}), and from 0.2 to 71.4 mg C m^{-3} d^{-1} (mean ± S.D. = 22.4 ± 21.1 mg C m^{-3} d^{-1}) in temperate lakes. Hypolimnetic R was significantly lower in boreal lakes, when excluding Lake 8 (82.0 mg C m^{-3} d^{-1}) that was a clear outlier in the boreal lakes group (Wilcoxon; $p = 0.0026$).

Figure 3.1A shows the average annual pattern in pelagic respiration for the 4 temperate lakes. R tended to decline during winter, and was significantly higher at the beginning compared to the end of the ice-cover period (Wilcoxon; $p = 0.0209$; Figure 3.1A), and tended to increase towards the end of the summer. Hypolimnetic respiration rates of the temperate lakes were significantly lower than surface rates (Wilcoxon; $p = 0.0043$). The mean respiration rates standardized at 10°C ($\bar{R}_{std}$, Figure 3.1B) were less variable throughout the year (variation

coefficient = 21%), although the winter decline is more pronounced with these data (Figure 3.1B). In addition, the respiration rates for the hypolimnion were much closer than those of the epilimnion when standardized for temperature, and showed a large peak in the early fall (Figure 3.1B). Figure 3.1C shows the average and range in mean pelagic respiration rates standardized for temperature ($\overline{R}_{std}$), for all lakes and for the different periods. Hypolimnetic $\overline{R}_{std}$ was on average 51% lower than surface rates during the same period, and within the same range of winter $\overline{R}_{std}$. The highest $\overline{R}_{std}$ were recorded during fall mixing.

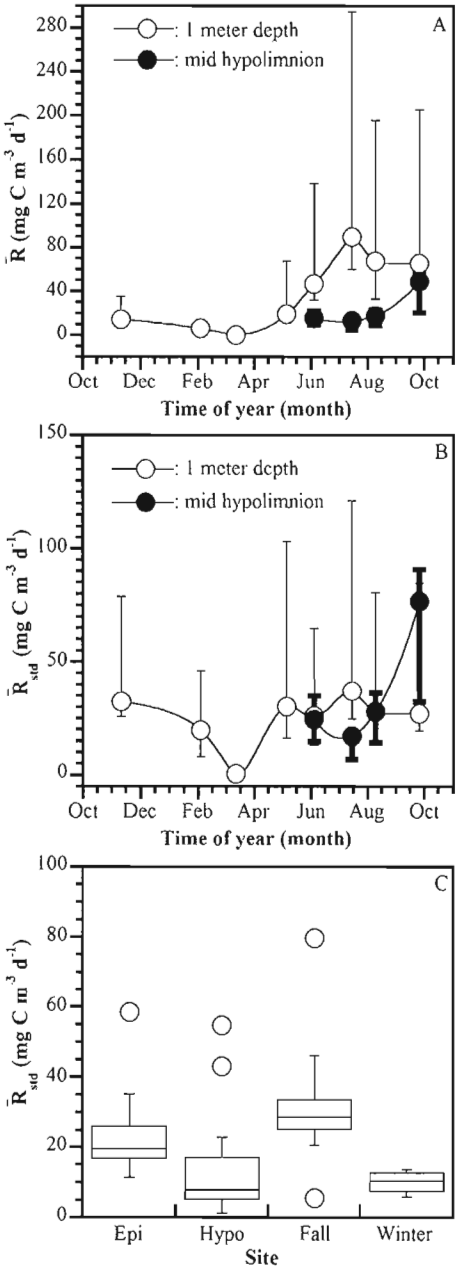

Figure 3.1 Annual cycle of pelagic respiration in temperate lakes for gross data (A) and for data standardised to a temperature of 10°C (B). Bars represent the data range and dots correspond to the mean respiration rate for each sampling month. Panel C shows the pelagic respiration standardised at 10°C (R_{std}) for lakes of both regions, in the epilimnion (Epi), in the hypolimnion (Hypo), during fall mixing (Fall) and during the ice cover period (Winter).

3.5.4 Winter and hypolimnetic ΔDOC

The rates of decline of DOC in the water column of ice-covered lakes (winter ΔDOC) ranged from 1.5 to 16.0 mg C m^{-3} d^{-1} (mean 6.2 ± 5.0 mg C m^{-3} d^{-1}, Lake 2 excluded). Lakes 34, 66 and EM-320 were only sampled once during the ice cover period thus winter ΔDOC are not available for these lakes. There was an overlap between winter ΔDOC (measured in most lakes) and winter pelagic respiration rates (measured only in 4 lakes), although the former tended to be on average higher and more variable (Figure 3.2A). ΔDOC in the hypolimnia ranged from 2.1 to 42.9 mg C m^{-3} d^{-1} (mean 14.5 ± 12.7 mg C m^{-3} d^{-1}), and were on average higher than winter ΔDOC. There was also a complete overlap between ΔDOC and $\bar{R}$ in the hypolimnion (Figure 3.2B).

3.5.5 Winter and hypolimnetic ΔCO_2 and ΔDIC

Total CO_2 accumulation rates during winter ($W\tau\Delta CO_2$; Figure 3.2A) ranged from 3.5 to 24.5 mg C m^{-3} d^{-1} (mean 12.0 ± 4.5 mg C m^{-3} d^{-1}), and were within the range of total hypolimnetic CO_2 accumulation rates ($H\tau\Delta CO_2$; 2.1 to 39.4 mg C m^{-3} d^{-1}, mean 19.7 ± 10.1 mg C m^{-3} d^{-1}; Figure 3.2B). The rate of DIC accumulation during winter (ΔDIC, Table 3.1) ranged from 3.2 to 22.7 mg C m^{-3} d^{-1} (mean 10.7 ± 5.3 mg C m^{-3} d^{-1}; Lakes 66 and 2 excluded). In the four temperate lakes, DIC accumulation rate in the summer hypolimnia ranged from 4.8 to 38.6 mg C m^{-3} d^{-1} (mean 21.6 ± 14.5 mg C m^{-3} d^{-1}, Table 3.1). The rate of DIC accumulation in the summer hypolimnia were not estimated in the boreal lakes because DIC measurements were made only where isotopic analyses where conducted. Considering all available winter and summer hypolimnetic ΔDIC, there was a strong positive relationship between $W\tau\Delta CO_2$ and ΔDIC (SLS; r^2= 0.75; $p < 0.0001$; n= 17; slope = 1.01 ± 0.149; intercept = -0.70 ± 2.41; Lakes Bowker, 2 and 66 excluded). $W\tau\Delta CO_2$ was on average two-fold higher than ΔDOC, and there was a strong positive relationship between winter ΔDOC and $W\tau\Delta CO_2$ ($r^2 = 0.80$; n = 13; $p < 0.0001$, Figure 3.2C). $H\tau\Delta CO_2$ completely overlapped with hypolimnetic ΔDOC (Figure 3.2B), but unlike for the winter, there was no relationship between the two.

Table 3.1 The rates of increase in DIC in the water column (ΔDIC), the rates of decline of DOC in the water column (ΔDOC), mean pelagic respiration rate ($\bar{R}$), estimation of winter benthic respiration from the method with pelagic respiration (SR^{M1}), and the method with ΔDOC (SR^{M2}), the winter benthic contribution from both methods (BC^{M1} and BC^{M2}), the ecosystem-level respiratory quotient (RQ) and the isotopic signature of the organic carbon respired (δ^{13}C-OC). Data are presented for the ice-cover period (W) and for the hypolimnion (H). The values in italic are likely underestimated (see discussion).

	ΔDIC (mg C m^{-3} d^{-1})		ΔDOC (mg C m^{-3} d^{-1})		$\bar{R}$ (mg C m^{-3} d^{-1})		SR^{M1} [SR^{M2}] (mg C m^{-2} d^{-1})	BC^{M1} [BC^{M2}] (%)	RQ		δ^{13}C-OC (‰)	
Lake	W	H	W	H	W	H	W	W	W	H	W	H
Bowker	11.1	4.8	1.6	2.14	3.6	9.8	*-1.4* [*39.3*]	- [*54*]	0.41	0.82	-	-28.8
Croche	14.7	16.0	1.5	9.1	1.8	14.5	64.8 [66.2]	88 [90]	0.85	0.79	-27.6	-31.2
Connelly	22.7	27.1	3.6	2.1	4.2	27.3	69.9 [74.8]	68 [73]	1.08	0.69	-24.4	-31.9
Bran de Scie	11.4	38.6	11.4	29.8	2.8	34.6	35.6 [*21.0*]	77 [*48*]	1.44	0.80	-21.7	-32.4
Natel	11.8	-	4.8	19.8	-	5.0	44.1 [35.1]	73 [58]	1.11	1.14	-25.2	-
Lake 60	3.2	-	3.1	14.8	-	1.4	22.0 [21.8]	55 [55]	1.10	1.32	-26.9	-
Labyrinthe	7.0	-	14.8	3.1	-	6.1	28.4 [*-16.9*]	70 [-]	0.98	0.87	-25.8	-
Lake 34	7.0	-	-	10.5	-	1.7	27.1 [-]	66 [-]	1.01	1.29	-25.4	-
Lake 8	9.1	-	4.5	42.9	-	5.7	28.4 [22.8]	77 [66]	1.09	1.28	-24	-
Brendan	9.5	-	4.3	2.8	-	17.9	33.5 [29.0]	74 [64]	1.00	1.35	-21.5	-
Lake 40	11.8	-	4.7	23.3	-	9.5	39.1 [32.3]	74 [61]	0.79	1.46	-23.8	-
Mistumis	5.8	-	4.4	14.0	-	5.3	15.1 [12.4]	70 [57]	0.99	1.27	-27.5	-
EM-320	6.1	-	-	-	-	7.0	23.0 [-]	76 [-]	1.03	-	-28.2	-
Lake 11	18.7	-	16.0	-	-	12.2	35.0 [*13.9*]	87 [*35*]	1.23	-	-26.7	-
Lake 2	87.4	-	33.3	-	-	-	82.4 [*37.0*]	95 [*43*]		-	-	-
Lake 66	38.1	-	-	-	-	6.2	40.3 [-]	76 [-]	1.02	1.51	-23.1	-

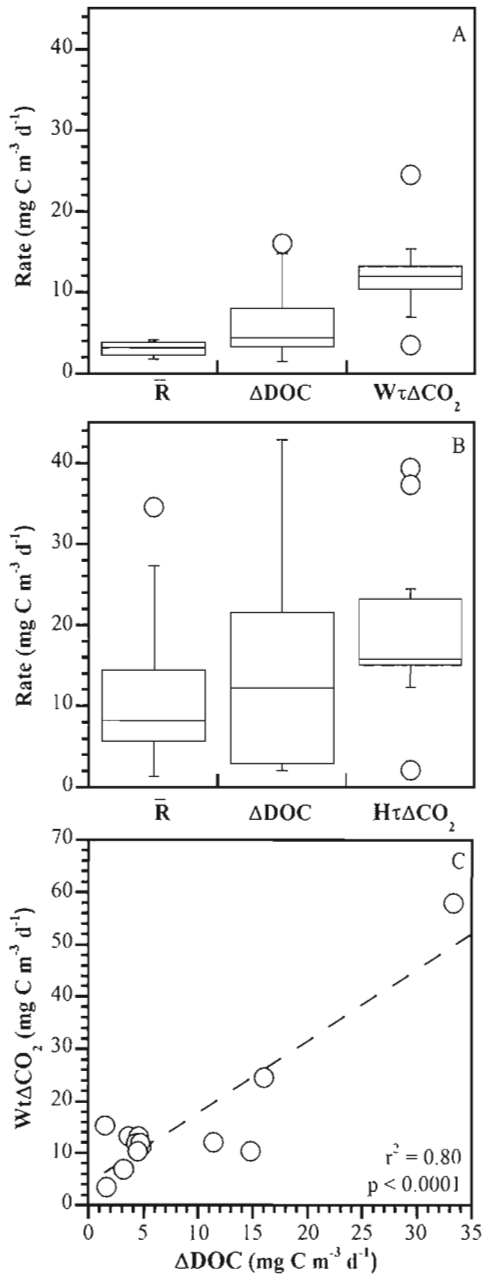

Figure 3.2 Distribution of mean pelagic respiration ($\bar{R}$), rate of decline of DOC (ΔDOC) and CO_2 accumulation rate in the water column during the ice cover period ($W\tau\Delta CO_2$, Panel A), and in the hypolimnion ($H\tau\Delta CO_2$, Panel B). $W\tau\Delta CO_2$ for Lake 2 is about 3-fold higher (see panel C) and is not shown on panel A. There is a relationship between the decline of DOC in the water column and $W\tau\Delta CO_2$ (C).

3.5.6 Winter benthic respiration

Our two alternative estimates of winter benthic respiration (winter R_{bent}) agreed well: Winter R_{bent} estimated using the mean winter pelagic respiration measured in temperate lakes applied to all lakes (Table 3.1 and Figure 3.3A) ranged from 15.1 to 82.4 mg C m^{-2} d^{-1} (mean 39.0 ± 19.1 mg C m^{-2} d^{-1}; Bowker excluded, see below). Estimates of Winter R_{bent} based on ΔDOC (Table 3.1 and Figure 3.3A) ranged from 12.4 to 74.8 mg C m^{-2} d^{-1} (mean 31.1 ± 18.1 mg C m^{-2} d^{-1}; Lake Labyrinthe excluded, see below). We obtained negative values of R_{bent} (Table 3.1) for lake Bowker using the first method, and for lake Labyrinthe using the ΔDOC method.

3.5.7 Hypolimnetic benthic respiration

Benthic respiration in the hypolimnion (hypolimnetic R_{bent}), calculated from the difference between hypolimnetic pelagic respiration and $H\tau\Delta CO_2$, ranged from -21.5 to 147.8 mg C m^{-2} d^{-1} (mean 45.7 ± 52.0 mg C m^{-2} d^{-1}) for boreal lakes, and from -26.6 to 7.1 mg C m^{-2} d^{-1} (mean -5.9 ± 18.1 mg C m^{-2} d^{-1}) for temperate lakes. These values are lower than direct measures of benthic respiration found in the literature (Pace and Prairie 2005) for a similar range of lake productivity, and together with the abundance of negative values, suggest that our hypolimentic R_{bent} are severely underestimated (see Discussion).

3.5.8 Benthic contribution to CO_2 accumulation

Benthic contribution to CO_2 accumulation in the hypolimnion was not estimated due the problems with the values of hypolimnetic R_{bent} (see above and Discussion). Winter benthic respiration (based on estimates of pelagic respiration from temperate lakes) accounted for 55.4 to 88.3 % (mean 74.0 ± 0.1 %, excluding Lake 2, see below) of the total CO_2 accumulation during the ice cover period (Table 3.1 and Figure 3.3B). The benthic contribution in Lake 2 was 94.6%, but this lake has a water column of less than one meter in

depth. The benthic contribution estimated on the basis of ΔDOC ranged from 35.0 to 90.2 % (mean 58.6 ± 14.4 %), excluding Lakes Labyrinthe, for which we had problems in the calculation of R_{bent}, and Lake 2, which has a water column of less than one meter depth during winter. The apparent contribution of R_{bent} in Lake 2 was surprisingly low (43%) when using the ΔDOC method, suggesting problems with either the estimates of ΔDOC (see Discussion) and/or of ΔCO_2. The contribution of winter benthic respiration to $W\tau\Delta CO_2$ (based on measurements of pelagic respiration of temperate lakes and $W\tau\Delta CO_2$) was negatively related to mean depth ($r^2 = 0.37$; n = 15; p = 0.0164; Figure 3.4A) and lake area ($r^2 = 0.38$; n = 15; p = 0.0140; Figure 3.4B). These relationships were not found when using estimates based on ΔDOC as a measure of R.

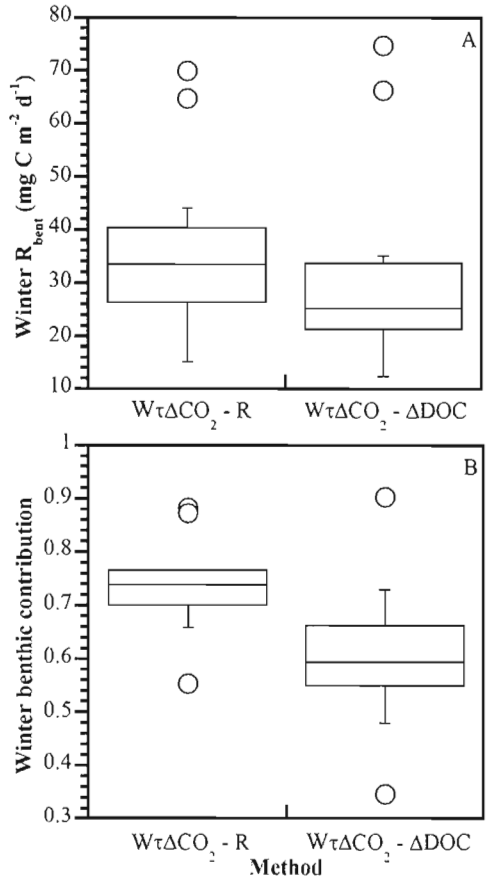

Figure 3.3 Winter benthic respiration (R_{bent}), estimated from 1) total CO_2 accumulation and pelagic respiration of the temperate lakes applied to all lakes ($W\tau\Delta CO_2$ - R) or 2) total CO_2 accumulation and the rate of decline of DOC in the water column ($W\tau\Delta CO_2$ - ΔDOC). Panel B shows winter benthic contribution to total CO_2 accumulation estimated from both methods. Lake 2, Labyrinthe and Bowker are excluded (see results).

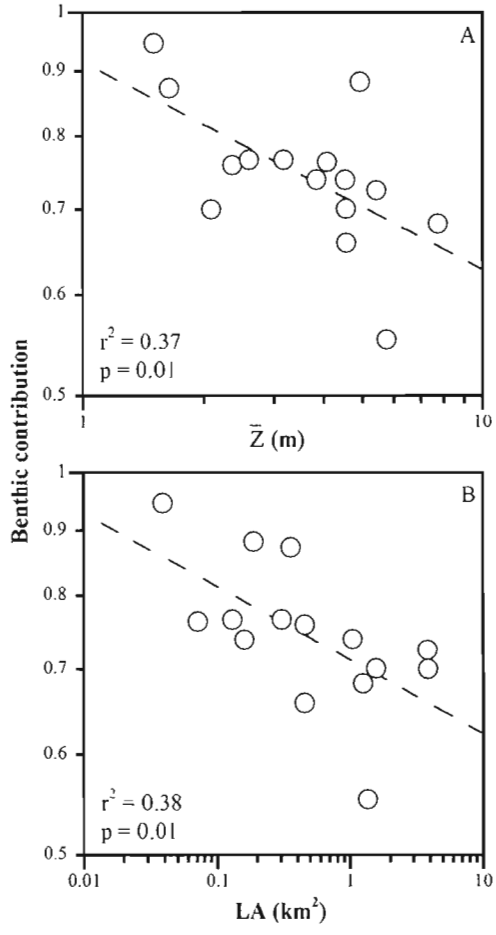

Figure 3.4 Winter benthic contribution (estimated from total CO_2 accumulation and pelagic respiration of the temperate lakes) versus mean depth ($\bar{Z}$, panel A) and lake area (LA, panel B).

3.5.9 Respiratory quotient

For logistical reasons we could not follow the change in the O_2 vertical profiles during winter, as we did for CO_2, but we nevertheless had simultaneous profiles of both O_2 and CO_2 for given dates in winter. Figure 3.5A shows a typical mid-winter vertical profile of CO_2 and O_2 (from Lake Brendan), where there was a strong inverse relationship between the vertical patterns in CO_2 and O_2 expressed as departures from saturation (Figure 3.5B). This was the case for all vertical profiles taken under the ice and in the hypolimnion, in all lakes (Orthogonal regressions, r were always > 0.85), and the resulting slopes were used to estimate ecosystem-level RQ. Figure 3.5C shows the resulting winter and hypolimnetic respiratory quotients (RQ). Winter RQs ranged from 0.41 to 1.44 (mean 1.01 ± 0.22), and hypolimnetic RQs had a very similar range, from 0.69 to 1.51 (mean 1.10 ± 0.28).

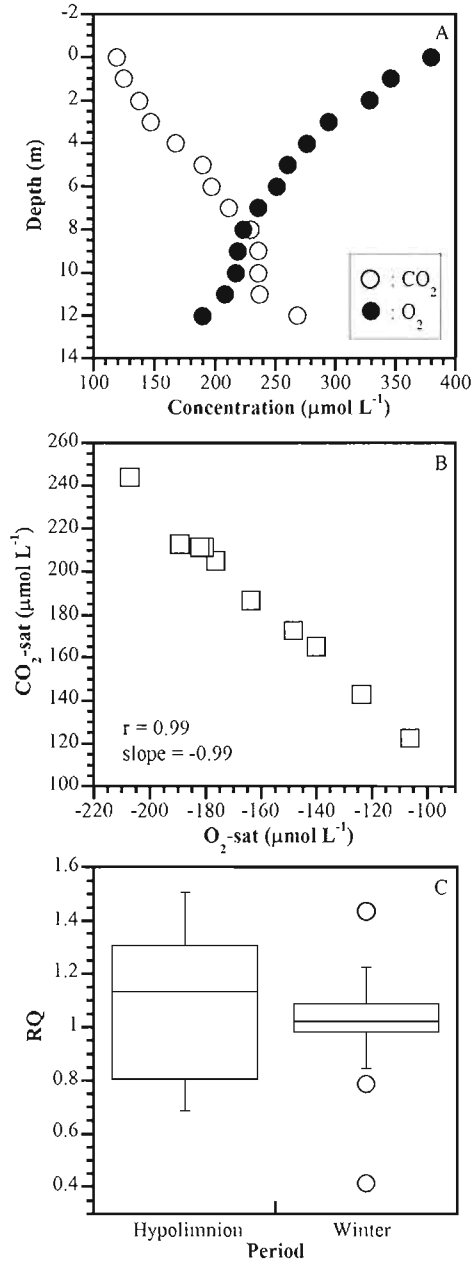

Figure 3.5 Example of a winter CO_2 and O_2 profile (A), and an example of an orthogonal regression of CO_2 and O_2 departures from saturation (CO_2-sat and O_2-sat, panel B) for Lake Brendan during the month of March 2008. The slope of this regression is used as the ecosystem-level respiratory quotient (RQ). The resulting RQs for all lakes, for the winter ice-cover and for the hypolimnion, are presented on panel C.

3.5.10 Isotopes signature

The $\delta^{13}C$ of DOC during winter (all lakes) and in the hypolimnion (four temperate lakes) was relatively invariant, and ranged from -28.8 to -26.0‰ (mean -27.0 ± 0.4‰). Ambient lake $\delta^{13}C$ of DIC had a much wider range of variation, from -24.0 to -4.1 ‰ (mean -13.8 ± 4.9 ‰). The concentration of DIC increased, and the isotopic signature of DIC tended to become more negative both with depth on a given date, and between dates during the winter ice-cover, and during summer stratification in the hypolimnion, thus generating a negative relationship with the inverse of DIC concentration. Figure 3.6A shows an example of a Keeling plot (for Lake Brendan) which was generated by combining data from different depths taken at successive times. All lakes had strong negative Keeling relationships (SLS; r^2 always > 0.85), and the depth patterns agreed well with the temporal patterns in the $\delta^{13}C$ versus 1/DIC relationship (Figure 3.6A).

The intercepts of the Keeling plots ($\delta^{13}C$-OC) were very different between hypolimnia and ice-covered lakes: $\delta^{13}C$-OC for hypolimnia (of temperate lakes only) ranged from -32.4 to -28.8 ‰ (mean -31.1 ± 1.6 ‰, Figure 3.6B), whereas $\delta^{13}C$-OC estimated for the winter ice cover period ranged from -27.6 to -21.7‰ (mean -24.6 ± 2.9 ‰) for the same temperate lakes; the latter had the same range of winter $\delta^{13}C$-OC as the boreal lakes, which ranged from -28.2 to -21.5 ‰ (mean -25.3 ± 2.0 ‰, Figure 3.6B). Overall, the hypolimnetic $\delta^{13}C$-OC was significantly different from the winter $\delta^{13}C$-OC (Wilcoxon; $p = 0.0029$). We could not construct a winter Keeling plot for Lake Bowker because the changes in DIC and $\delta^{13}C$ were very small and erratic. For the three lakes for which hypolimnetic and winter isotopic data were available (Lakes Connelly, Croche and Bran de Scie), there was a strong negative relationship between winter and hypolimnetic $\delta^{13}C$-OC (Figure 3.6C), i.e. lakes that had a lighter $\delta^{13}C$-OC during summer hypolimnia tended to have a heavier δ^{13}-OC during winter.

The Keeling intercepts were strongly related to the rate of CO_2 accumulation, albeit the patterns for winter and summer were diametrically different: $W\tau\Delta CO_2$ was positively related to $\delta^{13}C$-OC (Figure 3.7A), whereas $H\tau\Delta CO_2$ was negatively related to $\delta^{13}C$-OC (Figure

3.7B). There was an overall positive relationship between the ecosystem-level RQ and the Keeling plot intercept (Figure 3.7C), and both hypolimnetic and winter samples fit the same general relationship.

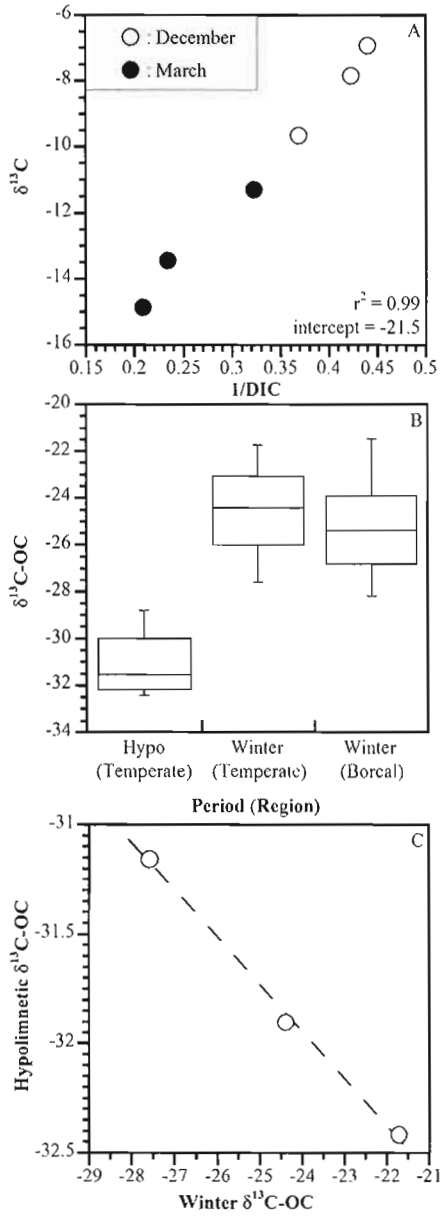

Figure 3.6 Example of a Keeling plot for Lake Brendan during the ice cover period (panel A). Measures of the isotopic signature in $\delta^{13}C$ of DIC were done at three depths during each sampling (December and March), and the variation of the $\delta^{13}C$ at different depths agreed well with the variation between sampling dates (panel A). The intercepts of the Keeling plots are assumed to represent the $\delta^{13}C$ of the organic matter respired ($\delta^{13}C$-OC) and are shown on panel B (Bowker and Lake 2 excluded, see results). Winter $\delta^{13}C$-OC were significantly higher than the hypolimnetic $\delta^{13}C$-OC (panel B; Wilcoxon; $p < 0.005$). There was a relationship between winter and hypolimnetic $\delta^{13}C$-OC (panel C) for the lakes for which we had data from both periods.

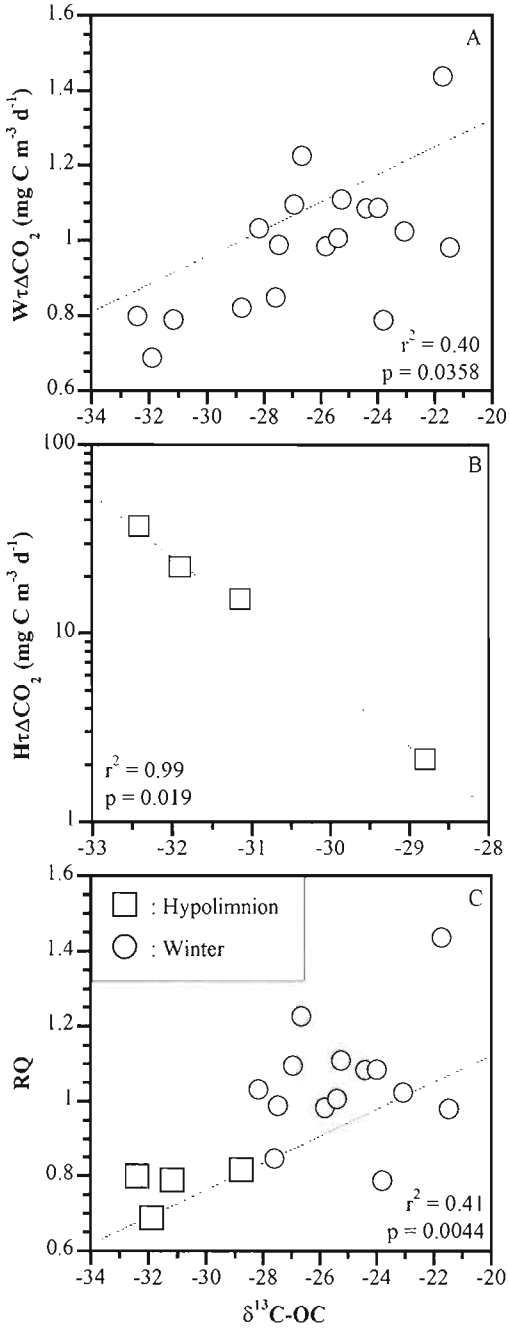

Figure 3.7 Rate of CO_2 accumulation during winter ($W\tau\Delta CO_2$, panel A) and in the hypolimnion ($H\tau\Delta CO_2$, panel B) in function of the isotopic signature of the organic carbon respired ($\delta^{13}C$ -OC), and the ecosystem-level RQ in function of the winter and hypolimnetic ($\delta^{13}C$–OC, panel C).

3.6 Discussion

In a previous study we have shown that the accumulation of CO_2 under the ice cover and in the summer hypolimnion of stratified lakes is quantitatively important relative to the annual CO_2 budget of these lakes (Ducharme-Riel et al. submitted). It has often been assumed that this CO_2 build up has a metabolic origin but there are very few empirical observations of this. In this study, we show several independent lines of evidence that support the assumption that under-ice and hypolimnetic CO_2 production in these lakes is dominated by heterotrophic metabolism. The first evidence is the strong coupling (orthogonal regression; $r > 0.9$) between O_2 and CO_2 departure from saturation with depth (Figure 3.5), from which were derived the ecosystem-level RQs, for both winter and summer hypolimnion. The second evidence is the direct measurements of pelagic respiration during those periods (figure 3.1), which demonstrate that water column metabolism contributes significantly to the CO_2 build-up. The third evidence is the strong coupling ($r^2 = 0.8$) between the DOC decline and the total CO_2 accumulation during winter ice cover (Figure 3.2C). This coupling was not found for the hypolimnion, but this is not surprising because summer hypolimnetic DOC concentrations may be affected by other processes, such as partial mixing of the water column, DOC flocculation (von Wachenfeldt et al. 2008; von Wachenfeldt and Tranvik 2008), and higher groundwater DOC inputs, and thus the patterns of change in DOC are less clear than during winter ice cover, and less representative of microbial degradation per se. In the next sections we discuss the pathways that generate this CO_2, the sources of organic matter that fuel these pathways, and how the ecosystem-level RQ varies across lakes.

3.6.1 Patterns in metabolism: Pelagic respiration

This study is among the few that has reported a complete annual cycle of pelagic respiration (Figure 3.1) that includes both surface and hypolimnetic measurements. For temperate lakes (Figure 3.1A), mean winter pelagic respiration (winter $\bar{R}$) and summer hypolimnetic $\bar{R}$

corresponded to 5 and 34% of the summer epilimnetic $\bar{R}$, respectively. For boreal lakes, hypolimnetic $\bar{R}$ represented 22% of the mean epilimnetic respiration. Differences in water temperature seem to be the main driver of seasonal variability (Apple et al. 2006). Indeed, when pelagic respiration rates of both boreal and temperate lakes were standardised at 10°C, winter and hypolimnetic rates both converged within the same range (Figure 3.1C), and over the more complete annual cycle of pelagic respiration available for temperate lakes (Figure 3.1B), the average surface and hypolimnetic respiration rates were less variable and overlapped once they were standardized for temperature (CV = 21%).

However, when all lakes are considered together, respiration in the epilimnion and during fall mixing was on average higher than winter and hypolimnion, even after temperature standardization (Figure 3.1C), and there was an extremely low average rate recorded at the end of the winter (temperate lakes only, Figure 3.1B), and a peak at the end of summer stratification suggesting a significant contribution of other variables. Previous studies in some of these same lakes have revealed high microbial mortality and significant declines in bacterial production towards the end of the winter ice cover, possibly due to depletion of labile organic matter (Fauteux et al. Submitted; Maurice et al. 2010), which could be linked to the observed drop in the respiration rates at the end of the winter ice cover. Higher rates of primary production in the epilimnion, and perhaps also the mixing of nutrient-rich hypolimnetic waters with organic matter-rich surface waters during fall turnover, may explain the overall higher rates in the epilimnion and during fall turnover, when considering lakes of both regions (Figure 3.1C). The peak in the average respiration rate towards the end of the summer stratification (Figure 3.1B), due to the higher respiration rates in the hypolimnion of the two most productive lakes (Lake Connelly and Bran de Scie), may be explained by higher exports of labile organic matter from a surface algal bloom (Baines and Pace 1994) and/or by the hypoxic conditions in the hypolimnion (see Results) that favour higher bacterial abundance and production (Cole and Pace 1995).

3.6.2 Patterns in metabolism: DOC consumption

Lake DOC lability and consumption rates are fundamental properties of these aquatic systems, and have generally been measured using in vitro bioassays (del Giorgio and Davis 2003; Søndergaard and Middelboe 1995). It is thus interesting to compare the ecosystem-level ΔDOC that we determined here, with in vitro ΔDOC reported for similar types of lakes. Our rates, standardized for temperature, fit well the patterns of long-term DOC consumption rates that have been observed in bioassays (del Giorgio and Davis 2003). For example, Guillemette and del Giorgio (in press) carried out 4-week DOC bioassays on temperate lakes of the same region, and reported initial rates of DOC consumption (at 20°C) in the order of 20 to 30 mg C m^{-3} d^{-1}. These authors also reported a steep decline in DOC consumption rates beyond the first few weeks of incubation. Our rates of DOC consumption, standardized to 20°C using a Q_{10} of 2 (Raymond and Bauer 2000), ranged from 3 to 28 mg C m^{-3} d^{-1} for both winter and summer hypolimnia, and are well within what would be expected for an incubation lasting several months, as is the case for the winter ice cover and stratification period in these lakes.

Overall it would appear that during summer stratification, and especially during winter ice cover, the lakes essentially function as reactors of existing DOC. However, some of our observations suggest that winter ΔDOC may be affected by processes other than metabolism alone, at least in some lakes: DOC samples from the last winter sampling of Lake Labyrinthe, Lake Bran de Scie, Lake 11 and Lake 2 were almost impossible to filter through a 0.45 μm pore capsule (capsules clogged with 1 to 10 ml), while at the beginning of winter, over 40 ml of water from these lakes were easily filtered with a single capsule. These observations suggest that there was an increase in colloidal or particulate matter in the water column towards the end of the winter, most likely due to precipitation of DOC in some of the lakes (von Wachenfeldt and Tranvik 2008). Interestingly, these four lakes had the highest ΔDOC (14.8, 11.4, 16.0 and 33.3 mg C m^{-3} d^{-1}, respectively), suggesting that the actual DOC consumption may have been overestimated. When excluding the above lakes from the mean winter ΔDOC, mean winter pelagic respiration (3.1± 1.0 mg C m^{-3} d^{-1}) and ΔDOC (new mean

± S.D. = 3.6 ± 1.3 mg C m^{-3} d^{-1}; n=10) were remarkably similar. Thus it would appear that in some lakes, winter ΔDOC may result in an overestimation of the actual winter pelagic respiration rates, but in most lakes, these two estimates are in excellent agreement (Figure 3.2A). Interestingly, there was a convergence in winter respiration rates and winter ΔDOC in these lakes, which otherwise differed greatly in all other aspects (Figure 3.2A). Export of DOC to lakes via the tributaries may also influence the ΔDOC during winter. However, the importance of DOC inputs to lakes via tributaries during the ice cover period is poorly known (see further work by Vachon and del Giorgio). A study on boreal catchment suggests that TOC exports by streams may be lower during winter (from 7 to 24% of total annual exports) compared to the other periods of the year (Laudon et al. 2004).

3.6.3 Patterns in metabolism: Benthic respiration

For both regions, our estimates of benthic respiration in summer hypolimnia (hypolimnetic R_{bent}) are lower than direct measurements of sediment respiration reported in the literature for a similar range of lake morphometry and productivity (Pace and Prairie 2005). This suggests that our approach probably underestimated summer hypolimnetic R_{bent}, and that indirect estimates of benthic respiration for the hypolimnion using total CO_2 accumulation and pelagic respiration may not be an appropriate method especially in shallower lakes where primary production and partial mixing during high wind conditions may result in the loss of accumulated hypolimnetic CO_2. Our estimation of CO_2 accumulation in the hypolimnion thus represents a net CO_2 accumulation, which is less appropriate to estimate R_{bent} by difference.

Winter benthic respiration (winter R_{bent}) calculated as the difference between ΔCO_2 and ΔDOC or pelagic respiration were in a similar range as those reported in Pace and Prairie (2005) for a similar range in lake TP, when standardized for temperature. The negative estimate of R_{bent} for Lake Bowker may be due to an underestimation of its $W\tau\Delta CO_2$ (Ducharme-Riel et al. submitted), whereas overestimation of R (see Discussion, DOC

consumption section) may cause the negative R_{bent} obtained for Lake Labyrinthe when using ΔDOC as a proxy for pelagic respiration.

Winter benthic respiration accounted for an average of 59 % (method with ΔDOC) to 74% (method using pelagic $\bar{R}$) of total winter under-ice CO_2 accumulation (Table 3.1), which is in accordance with previous results obtained by Karsslon et al. (2008) for a shallow subarctic clear water lake (80%). The negative relationships between winter benthic contribution and mean depth (Figure 3.4A) or lake area (Figure 3.4B) are expected, smaller lakes having a higher sediment area to water volume ratio. The lake studied by Karlsson et al. (2008) also fit well in these relationships. In our study, smaller lakes tended to have higher TP and DOC concentrations, and likely had a greater amount of organic matter and nutrients accumulated in the sediments, which could drive the above relationships. However there was no relationship between winter R_{bent} and TP or chlorophyll *a*, suggesting that morphometric aspects are the main drivers of these patterns.

There was a remarkable convergence in the contribution of benthic respiration to winter CO_2 accumulation across lakes (CV < 25% for both methods; Figure 3.3B), despite the wide range in lake morphometry. The components that were used to estimate benthic contribution to winter CO_2 accumulation, i.e. pelagic respiration (or ΔDOC) and total CO_2 accumulation, also showed very little variability across lakes (CV of 29-90%, or 29-33% when excluding lakes for which we had filtration issues), and the resulting winter R_{bent} (CV of 49% to 62%, Figure 3.3A) was also relatively invariant in comparison to summer processes reported in the literature for some of these lakes (example: CV of 300% for summer planktonic respiration for a similar range of TP, see Marchand 2007). Overall, our results show that lake metabolic rates tend to converge during the winter ice cover period, temperature probably playing a more important role than cross-lake differences in the overall trophic status, as it had been previously hypothesized (Felip et al. 1996; Nedwell 1999). Despite the lack of solid estimates of benthic respiration during summer stratification, the evidence suggests that the contribution of benthic metabolism is more important during the ice cover period. Benthic respiration accounted for over half of the total CO_2 accumulated under the ice cover, and in a study that included some of these same lakes, sediment respiration accounted for an average

of 5 to 33% of total lake mineralization during the open water season, for a similar range of lake trophic status (den Heyer and Kalff 1998).

3.6.4 Sources of organic carbon supporting CO_2 production

As discussed above, the evidence suggests that the CO_2 accumulated during winter and in the hypolimnion is overwhelmingly of metabolic origin. The increase of DIC in the water column during the period of winter ice-cover and in the hypolimnion is of the same magnitude as the increase in CO_2 (slope not significantly different from one), suggesting that the former is directly due to the latter, which is important for the interpretation of the Keeling plots. Exceptions are Lake 66 and Lake Bowker, were the ΔDIC were higher than the $\tau\Delta CO_2$. Further, methane oxidation produces CO_2 with a very light $\delta^{13}C$ signature (Miyajima et al. 1997), potentially biasing our isotopic results, but exclusion of samples taken during periods of hypoxia and anoxia did not change results substantially ($< \pm$ 0.1 ‰). The above support the assumption that the Keeling plot intercepts likely correspond to the isotopic signature of the organic carbon consumed ($\delta^{13}C$-OC). We did not determine the signature of the potential endpoint sources of the organic carbon, and cannot thus construct a quantitative isotopic mass balance. We can however, use published information for similar types of lakes (France 1995; Hecky and Hesslein 1995; McCallister and del Giorgio 2008) to obtain a likely range of $\delta^{13}C$ signatures for benthic algae and macrophytes (-27 to -17 ‰), planktonic algae (-43 to -29‰), and from terrestrial plant material (-29 to -26‰), which we can use to at least place our measurements in context (see figure 3.8).

There is now widespread evidence that terrestrially-derived OC fuels a significant fraction of summer metabolism in both temperate (Kritzberg et al. 2004; McCallister and del Giorgio 2008) and boreal (Algesten et al. 2003; Jonsson et al. 2001; Karlsson et al. 2007) lakes. The relative invariance of $\delta^{13}C$ of DOC that we observed seasonally and across lakes (27.0 $\pm$ 0.4‰) suggests that a large refractory organic matter pool composed mainly of carbon of terrestrial origin dominates the bulk DOC in all of the studied lakes. Autochthonous organic

carbon of phytoplankton origin, which usually has a lighter signature in $\delta^{13}C$ than terrestrial carbon (del Giorgio and France 1996), does not appear to build up in the bulk DOC pool, probably due to its high lability and turnover (Kritzberg et al. 2004). Thus, pelagic primary production does not persist in the water column for long, and neither does it lead to a significant accumulation of DOC which can then fuel metabolism later in the year, for example, during winter ice cover. Given the seasonal invariance of the isotopic signature of DOC across these lakes, there is no reason to assume that terrestrial OC does not also support a significant proportion of metabolism during winter and summer stratification in all lakes as well. In the absence of other sources, we would thus expect that the isotopic signature of the winter and hypolimnetic $\delta^{13}C$-OC would converge to that of terrestrial OC across lakes. Alternative sources of OC would then simply dilute the terrestrial signature and result in deviations of $\delta^{13}C$-OC around the mean value for the latter.

In this regard, our results show 1) major divergences from the terrestrial signature in both winter and hypolimnion, and 2) a strongly contrasting seasonal pattern of $\delta^{13}C$-OC between winter ice cover and summer hypolimnion. Figure 3.8 shows the $\delta^{13}C$-OC as a function of summer chlorophyll concentration; we have also superimposed in this figure the approximate ranges expected for phytoplankton, terrestrial and benthic algae/macrophyte OC. We had hypothesized that the divergence from the terrestrial signature should increase with productivity (i.e. chlorophyll), and this was indeed the case for hypolimnetic $\delta^{13}C$-OC, which was consistently lighter than terrestrial OC ($\delta^{13}C$-OC between -33 to 28.5‰), and become progressively more depleted (more algal) with increasing chlorophyll. This pattern suggests a pelagic primary production signature in the hypolimnetic $\delta^{13}C$-OC diluting the terrestrial signature, and thus a direct connection between surface processes and summer hypolimnetic metabolism (Baines and Pace 1994). In contrast, the average winter $\delta^{13}C$-OC for about half of the lakes was consistently heavier relative to terrestrial organic C (Figure 3.6B), and this pattern was similar for both temperate and boreal lakes. These heavier signatures relative to the terrestrial OC suggest a contribution of benthic algae (see also Karlsson et al. 2008) and/or littoral macrophytes. The other half of winter $\delta^{13}C$-OC were not significantly different from the signature of terrestrial organic C. The departure of winter $\delta^{13}C$-OC from the

terrestrial signature was clearly not related to summer trophic status, and should in theory be linked to patterns in benthic production in these lakes, yet winter isotopic patterns were not explained by any of the morphometric or chemical variables that have previously been linked to benthic production (Vadeboncoeur et al. 2008).

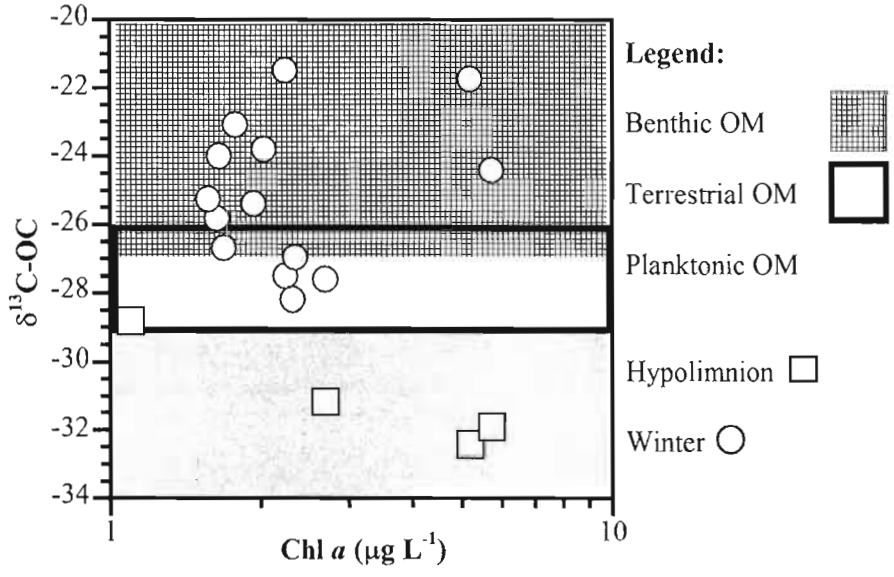

Figure 3.8 Winter and hypolimnetic signature in $\delta^{13}C$ of the organic carbon respired ($\delta^{13}C$-OC) versus mean chlorophyll *a* (Chl *a*). The ranges in $\delta^{13}C$ of the different types of organic matter, i.e. benthic (Benthic OM), terrestrial (Terrestrial OM) and phytoplanktonic (Planktonic OM) organic matter reported in the literature, for similar types of lakes are shown (France 1995; Hecky and Hesslein 1995; McCallister and del Giorgio 2008).

Thus, in many lakes of our study, the baseline terrestrial signature is diluted by other sources, but these sources appear to be fundamentally different between summer and winter. Benthic photosynthesis is not likely to be significant under the thick ice cover of these lakes, rather it is more likely that benthic primary production from the previous open water seasons persists and sustains a significant portion of total benthic winter respiration, in agreement with the results shown for a clear water subarctic lake by Karlsson et al. (2008). The benthic signal, which probably originates from sediment respiration, is probably diluted during the open water season by both phytoplankton production and new inputs of terrestrial OC, and becomes quantitatively important only in the winter when these other pathways are at their lowest. This in turn confers a certain level of stability to ecosystem metabolism in these northern lakes.

Interestingly, the few lakes for which we had both winter and hypolimnetic δ^{13}C-OC show a clear gradient of dominance of allochthonous and authochthonous OC: The lake that had the strongest phytoplankton signature in the summer hypolimnion, also had the strongest benthic algal signature during the winter (Figure 3.6C). This implies that there are lakes where authochthonous OC plays a major role in shaping both winter and hypolimnetic CO_2 dynamics, but that the main source of authochthonous C varies seasonally. Likewise, the lake that had the strongest terrestrial signature in winter also had a strong terrestrial signature in the hypolimnion (Figure 3.6C), suggesting that this is a category of lake where CO_2 dynamics are overwhelmingly dominated by allochthonous inputs. This in turn suggests that although winter and hypolimnetic rates of metabolism and CO_2 accumulation appear to be uncoupled (Ducharme et al. submitted) our limited isotopic data suggest that there may be a closer coupling in terms of δ^{13}C-OC.

3.6.5 Links between sources of OM, ecosystem metabolism, and gas dynamics in lakes during winter ice cover and summer hypolimnia

We have shown that there was a strong coupling between CO_2 and O_2 along vertical profiles, which resulted in a range of apparent ecosystem-level RQs between 0.4 and 1.4 (Figure

3.5C), well within the range expected for aerobic metabolism of the major classes of organic substrates (Williams and del Giorgio 2005). Our values also agree with the few existing empirical measurements of lake RQ for aerobic sediments and water column (Baehr and Degrandpre 2002; Fukushima et al. 2000; Hanson et al. 2003). There are several factors that may influence these ecosystem-level RQs, including the type of substrate preferentially consumed (Williams and del Giorgio 2005), the relative importance of sediment and water column processes, and the relative contribution of aerobic and anaerobic metabolism (Murray and Rich 1995; Rich 1980). Significant contributions of anaerobic pathways, or of groundwater inputs, should result in high RQs (above 1.5 to 2), which was not the case in our study. Likewise, a positive relationship between the relative importance of the sediments and the ecosystem-level RQs could be expected since anaerobic pathways occur predominantly in the sediments, yet we found no relationship between the benthic contribution to total CO_2 accumulation and RQs.

We did find, however, a significant relationship between the RQs and the isotopic signature of the organic carbon consumed (Figure 3.7C), which strongly points to a physiological basis for the variation in winter and hypolimnetic RQs, most likely driven by broad differences in the nature of the organic matter consumed. The consumption of organic carbon with a lighter $\delta^{13}C$ signature was apparently linked to lower RQs compared to organic carbon with heavier $\delta^{13}C$, thus determining a range of RQs according to the origin of predominant organic substrates : Benthic (RQ $\approx$ 1.2), terrestrial ($\approx$1) or planktonic algal carbon ($\approx$ 0.8).

In systems, such as lakes during winter ice cover, where metabolism dominates gas dynamics, these differences in RQ, driven by the sources of organic C metabolized, may profoundly influence the overall gas balance, even in systems dominated by aerobic processes. In addition, we have shown (Figure 3.7A and B) that the dominant sources of carbon fuelling winter and hypolimnetic metabolism are linked to the actual rates of CO_2 accumulation, and that the resulting winter and hypolimnetic CO_2 dynamics are important components of the annual C budget of northern lakes. Perhaps more importantly, the sources of C fuelling the underlying metabolism must be considered in any assessment of the net role of lakes as C sources or sinks, for while the accumulation of CO_2 derived from the respiration

of terrestrial OC contributes to the overall net heterotrophy of the lakes, and thus to their role as net sources of C to the atmosphere, the accumulation and subsequent emission of CO_2 derived from authochthonous sources does not represent a net source of C to the atmosphere, but rather a contemporary C loop.

4. CONCLUSION

4.1 CONTRUBUTIONS DE L'ÉTUDE AUX CONNAISSANCES SUR LA DYNAMIQUE DU CARBONE DANS LES LACS

4.1.1 Importance de l'hiver et de l'hypolimnion dans les émissions annuelles nettes de CO_2 (Article I)

La période du couvert de glace et l'hypolimnion estival sont des composantes souvent ignorées dans les bilans annuels de carbone des lacs mais notre étude démontre pourtant qu'elles sont des périodes d'accumulation significative de CO_2 contribuant à plus de 30% des émissions annuelles. L'importance relative de la période du couvert de glace sur les émissions annuelles nettes de CO_2 est plus grande dans les lacs oligotrophes et dans les lacs qui sont très productifs pendant la saison libre de glace. L'importance relative de l'hypolimnion estival sur les émissions annuelles nettes de CO_2 est plus grande dans les lacs plus profonds dans lesquels le volume hypolimnétique et la stabilité de la stratification sont plus grands.

4.1.2 Patrons d'accumulation de CO_2 (Article I)

L'approche que nous avons proposée, soit d'étudier deux composantes du cycle annuel des lacs de façon comparative, a permis d'approfondir nos connaissances sur la dynamique saisonnière du métabolisme lacustre dans des conditions in situ. La comparaison entre les deux périodes d'isolation, soit la période du couvert de glace et l'hypolimnion estival, montre qu'il y a une convergence des lacs en hiver, en termes d'accumulation de CO_2, par rapport à l'hypolimnion qui est plus variable. Cette convergence entre les lacs en hiver, qui sont pourtant très différents en termes de nutriments et de morphométrie, semble être attribuable à une moins forte association entre les processus hivernaux et le statut trophique du lac alors que les processus hypolimnétiques y demeurent davantage couplés. Pendant la saison libre de glace, la variation dans le degré de productivité des lacs est exprimée entre autre par des

différences en production primaire et en taux métaboliques. Sous le couvert de glace, la variation dans le degré de productivité n'est probablement pas autant exprimée étant donné un niveau de limitation semblable entre les lacs par la température et la lumière.

4.1.3 Outils d'intégration de l'accumulation hivernale dans les émissions annuelles de CO_2 (Article I)

Le premier article de notre étude fournit plusieurs relations permettant d'estimer de façon empirique l'accumulation de CO_2 pendant les périodes d'isolation. Toutefois, l'accumulation de CO_2 en hiver semble être une composante très peu variable du cycle annuel des lacs, du moins dans les lacs boréaux et tempérés de niveau oligotrophe à mésotrophe. Nous proposons donc une valeur moyenne de 8,3 ± 2,6 g C m^{-2} qui peut être intégrée au bilan d'émissions de CO_2 d'un lac afin d'inclure les accumulations de la période du couvert de glace dans les estimations. Les études désirant mesurer les émissions de CO_2 relative à l'accumulation hivernale devront considérer dans la planification de leur échantillonnage que le CO_2 accumulé pendant l'hiver sera émis dans l'atmosphère sur une période totalisant environ 30 jours suivant la fonte du couvert de glace et que les flux qui y sont associés seront probablement plus élevés dans les premiers jours suivant la fonte, étant donnée le plus fort gradient de concentration en CO_2 entre le lac et l'atmosphère.

4.1.4 Origine du CO_2 en hiver et dans l'hypolimnion (Article II)

Dans les écosystèmes aquatiques, on assume souvent que le CO_2 a une origine métabolique. Toutefois, il existe peu d'observations supportant cette hypothèse. Dans notre étude, plusieurs indices supportent que le CO_2 accumulé sous le couvert de glace et dans l'hypolimnion estival des lacs étudiés provient principalement des processus métaboliques (respiration). De façon générale, on peut conclure que le métabolisme semble être une source significative de CO_2 dans les lacs et que l'étude du métabolisme microbien peut contribuer à améliorer notre compréhension de la dynamique du CO_2 lacustre.

4.1.5 Dynamique saisonnière de la respiration pélagique (Article II)

Un nombre très restreint d'études ont mesuré la respiration pélagique dans un cycle annuel complet. Dans cette étude, nous avons mesuré la respiration pélagique en surface dans un cycle annuel complet, incluant la période du couvert de glace. De plus, nous avons mesuré la respiration pélagique dans l'hypolimnion lors de la stratification thermique estivale. Nos résultats montrent que la température semble être le principal modulateur de la variation saisonnière de la respiration pélagique, une conclusion aussi partagée par les travaux d'Apple et al. (2006) dans un système estuarien. Par contre, nos résultats pourraient indiquer qu'à certains moments de l'année, d'autres variables viennent influencer significativement la variation saisonnière de la respiration pélagique. Bien que nos données ne nous permettent pas d'identifier ces variables avec certitudes, les conditions en oxygène, une très grande ou très faible disponibilité en matière organique labile et en nutriments sont possiblement les variables secondaires qui ont des effets sur la variation saisonnière de la respiration pélagique vers la fin de la période du couvert de glace et de la stratification thermique estivale ainsi que lors du brassage automnale.

4.1.6 Importance du métabolisme benthique en hiver (Article II)

Plusieurs auteurs ont suggérés l'importance de la respiration benthique sur le métabolisme hivernal des lacs (Åberg et al. 2007) mais très peu d'études ont vérifié cette hypothèse (Karlsson et al. 2008). Dans les lacs de notre étude, le métabolisme benthique est responsable de plus de la moitié de l'accumulation de CO_2 sous le couvert de glace et cette proportion tend à être plus grande dans les petits lacs qui ont un ratio d'aire de sédiment plus élevé par rapport à leur volume d'eau en comparaison aux plus grands lacs. La forte contribution de la respiration benthique souligne l'importance de considérer les sédiments dans l'étude de la dynamique du CO_2 et ce, plus particulièrement pendant la période du couvert de glace où la respiration benthique semble avoir une plus grande contribution relative par rapport à la période libre de glace. Bien que nous n'ayons pas été en mesure d'estimer la contribution benthique pendant la stratification estivale, les valeurs rapportées dans la littérature

concernant la période libre de glace suggèrent que les sédiments contribuent davantage au métabolisme hivernal qu'au métabolisme hypolimnétique.

4.1.7 Sources de matière organique (Article II)

De nombreuses études ont démontré l'importance du carbone terrestre en tant que source alimentant la respiration dans les écosystèmes aquatiques d'eau douce. Le réservoir de DOC des lacs de la présente étude montre une signature en $\delta^{13}C$ clairement terrestre qui est très peu variable entre les lacs et saisonnièrement, ce qui suggère que cette source de carbone est relativement stable et qu'elle a probablement un temps de renouvellement très lent. Cette source de carbone doit donc être disponible pour alimenter la respiration mais elle est possiblement moins labile. Considérant la présence de la matière organique terrestre dans tous les lacs, les divergences entre la signature isotopique du carbone respiré et la signature du carbone terrestre devraient donc être interprétées comme une dilution du signal terrestre due à la contribution de d'autres sources de carbone organique alimentant la respiration. Dans l'hypolimnion de plusieurs des lacs étudiés, la signature isotopique du carbone organique respirée était appauvrit en ^{13}C par rapport au carbone d'origine terrestre, ce qui suggère que le carbone d'origine phytoplanctonique alimente de façon significative la respiration dans l'hypolimnion. Pendant la période du couvert de glace, la signature isotopique du carbone organique respiré n'était pas significativement différente du carbone terrestre dans environ la moitié des lacs. Toutefois, dans plusieurs lacs, la signature isotopique en $\delta^{13}C$ du carbone organique respiré pendant la période du couvert de glace était clairement enrichit par rapport au carbone terrestre, suggérant une contribution significative du carbone autochtone benthique pour alimenter la respiration sous le couvert de glace. Le fait de mesurer ces signatures benthiques dans le CO_2 respiratoire ne signifie pas que cette source de carbone soit consommée seulement pendant la période du couvert de glace. Nous suggérons plutôt que le carbone d'origine benthique est produit pendant la période libre de glace et consommé pendant toute l'année mais que sa signature n'est perceptible qu'en hiver étant donné la diminution de l'importance relative des autres sources, telle que le carbone d'origine phytoplanctonique, qui est également produit pendant la période libre de glace mais qui est

plus rapidement consommé et qui ne peut donc pas soutenir de façon significative le métabolisme hivernal.

4.1.8 Coefficient respiration à l'échelle du système (Article II)

Lorsqu'on convertit en unité de carbone les données de respiration mesurées à partir de la diminution d'O_2 en fonction du temps, on assume souvent un coefficient respiratoire (RQ) de 1, c'est-à-dire un ratio de 1 :1 entre la consommation d'O_2 et la production de CO_2. Il existe très peu d'observations directes supportant cette hypothèse. Dans cette étude, nous avons estimé in situ le RQ à l'échelle du lac. Dans les lacs oligotrophes à mésotrophes pour lesquels les processus anaérobiques ont une contribution relativement faible par rapport au processus aérobiques, les RQ sont en effet très près de 1 (moyenne : 1,05 ± 0,25). Il y a toutefois une variation dans les RQ (étendue : 0,4 à 1,5) et cette variation semble en partie expliquée par le type de carbone organique respiré.

4.2 PERSPECTIVES DE RECHERCHES FUTURES

L'approche isotopique suggère que la production primaire benthique est une source de carbone qui contribue significativement à soutenir la respiration dans de nombreux lacs ayant des concentrations en COD variées, même sous le couvert de glace, ce qui est une découverte relativement récente (voir aussi Karlsson et al. 2008). La production primaire benthique est une composante très peu étudiée dans les lacs, en partie due aux difficultés méthodologiques mais aussi parce que la production primaire dans la colonne d'eau est souvent considérée comme étant relativement plus significative. Lorsqu'on cherche à qualifier (net hétérotrophe versus net autotrophe) et quantifier le rôle des lacs dans les bilans de carbone à l'échelle régionale, il est primordial de s'intéresser aux sources de carbone qui alimentent la production de CO_2 dans les lacs. Les découplages spatiaux et temporels qui semblent exister entre la production autochtone du carbone organique et de sa subséquente respiration pourraient entraîner des biais dans notre perception des lacs à l'échelle régionale puisqu'une

portion significative du CO_2 produit semble provenir de carbone précédemment fixé dans le lac lui-même. Notre étude souligne l'importance d'inclure les différentes composantes du cycle annuel des lacs dans les bilans annuels de carbone et d'accorder davantage d'attention au processus benthiques, particulièrement dans les lacs qui sont relativement peu profonds.

5. BIBLIOGRAPHIE

Åberg, J., M. Jansson, J. Karlsson, K.-J. Nääs and A. Jonsson. 2007. Pelagic and benthic net production of dissolved inorganic carbon in an unproductive subarctic lake. *Freshwater Biology* **52:** 549-560.

Agbeti, M. D., and J. P. Smol. 1995. Winter limnology: a comparison of physical, chemical and biological characteristics in two temperate lakes during ice cover. *Hydrobiologia* **304:** 221-234.

Algesten, G., S. Sobek, A.-K. Bergström, A. Ågren, L. J. Tranvik and M. Jansson. 2003. Role of lakes for organic carbon cycling in the boreal zone. *Global Change Biology* **10:** 141-147.

Algesten, G., S. Sobek, A.-K. Bergström, A. Jonsson, L. J. Tranvik, and M. Jansson. 2005. Contribution of sediment respiration to summer CO_2 emission from low productive boreal and subarctic lakes. *Microbial Ecology* **50:** 529-535.

Amorocho J., and J. J. DeVries. 1980. A new evaluation of the wind stress coefficient over water surfaces. *Journal of Geophysical Research* **85**: 433-442

Apple, J. K., P. A. del Giorgio, and W. M. Kemp. 2006. Temperature regulation of bacterial production, respiration, and growth efficiency in a temperate salt-marsh estuary. *Aquatic Microbial Ecology* **43:** 243-254.

Ahrens, M.A., and R. H. Peters. 1991. Plankton community respiration: relationships with size distribution and lake trophy. *Hydrobiologia* **224:** 77-87.

Babin, J., and E. E. Prepas. 1985. Modelling winter oxygen depletion rates in ice-covered temperate zone lakes in Canada. *Canadian Journal of Fisheries and Aquatic Sciences* **42:** 239-249.

Baehr, M. M., and M. D. Degrandpre. 2002. Under-ice CO_2 and O_2 variability in a freshwater lake. *Biogeochemistry* **61:** 95-113.

Baines, S. B., and M. L. Pace. 1994. Relationship between suspended particulate matter and sinking flux along a trophic gradient and implications for the fate of planktonic primary production. *Canadian Journal of Fisheries and Aquatic Sciences* **51:** 25-36.

Barica, J., and J. A. Mathias. 1979. Oxygen depletion and winterkill risk in small prairie lakes under extended ice cover. *Journal of the Fisheries Research Board of Canada* **36:** 980-986.

Bédard, C., and R. Knowles. 1991. Hypolimnetic O_2 consumption, denitrification, and methanogenesis in a thermally stratified lake. *Canadian Journal of Fisheries and Aquatic Sciences* **48:** 1048-1054.

Bengtsson, L. 1996. Mixing in ice-covered lakes. *Hydrobiologia* **322:** 91-97.

Carignan, R., and D. R. S. Lean. 1991. Regeneration of dissolved substances in a seasonnally anoxic lake: The relative importance of processes occurring in the water column and in the sediments. *Limnology and Oceanography* **36:** 683-707.

Carignan, R., D. Planas, and C. Vis. 2000. Planktonic production and respiration in oligotrophic Shield lakes. *Limnology and Oceanography* **45:** 189-199.

Carlsson, P., and D. A. Caron. 2001. Seasonal variation of phosphorus limitation of bacterial growth in a small lake. *Limnology and Oceanography* **46:** 108-120.

Chambers, M. K., D. M. White, M. R. Lilly, L. D. Hinzman, K. M. Hilton, and R. C. Busey. 2008. Exploratory analysis of the winter chemistry of five lakes on the north slope of Alaska. *Journal of The American Water Resources Association* **44:** 316-327.

Charlton, M. N. 1980. Hypolimnion oxygen consumption in lakes: discussion of productivity and morphometry effects. *Canadian Journal of Fisheries and Aquatic Sciences* **37:** 1531-1539.

Christensen J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R. K. Kolli, W.-T. Kwon, R. Laprise, M. V. Rueda, L. Mearns, C. G. Menéndez, J. Räisänen, A. Rinke, A. Sarr, and P. Whetton. 2007. Regional Climate Projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller (editors). Cambridge (UK) and New York (USA): Cambridge University Press, p. 847-940.

Cimbleris, A. C. P., and J. Kalff. 1998. Planktonic bacterial respiration as a function of C: N: P ratios across temperate lakes. *Hydrobiologia* **384:** 89-100.

Clayton, J.S., and I. B. Marshall. 1972. Sols, 1972. 1: 15 000 000, In *Atlas du Canada.* En ligne. < http://atlas.nrcan.gc.ca/auth/francais/maps/archives/4thedition/environment/land/041_42 >. Consulté le 3 novembre 2010

Cole, J. J., and N. F. Caraco. 1998. Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF_6. *Limnology and Oceanography* **43:** 647-656.

Cole, J. J., N. F. Caraco, G. W. Kling, and T. K. Kratz. 1994. Carbon dioxide supersaturation in the surface waters of lakes. *Science* **265:** 1568-1570.

Cole, J. J., N. F. Caraco, W. H. McDowell, L. J. Tranvik, R. G. Striegl, C. M. Duarte, P. Kortelainen, J. A.Downing, J. J. Middelburg, and J. Melak. 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems* **10:** 171-184.

Cole, J. J., and M. L. Pace. 1995. Bacterial secondary production in oxic and anoxic freshwaters. *Limnology and Oceanography* **40:** 1019-1027.

Cole, J. J., and Y. T. Prairie. 2009. Dissolved CO_2. In: *The Encyclopedia of inland waters*, G. E. Likens [editor]. Oxford: Elsevier, p. 30-34.

Cornett, R. J., and R. H. Rigler. 1980. The areal hypolimnetic oxygen deficit: an empirical test of the model. *Limnology and Oceanography* **25:** 672-679.

————————. 1987. Vertical transport of oxygen into the hypolimnion of lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **44:** 852-858.

Cotner, J. B., T. H. Johengen, and B. A. Biddanda. 2000. Intense winter heterotrophic production stimulated by benthic resuspension. *Limnology and Oceanography* **45:** 1672-1676.

Crump, B. C., G. W. Kling, M. Bahr, and J. E. Hobbie. 2003. Bacterioplankton community shifts in an arctic lake correlate with seasonal changes in organic matter source. *Applied and Environmental Microbiology* **69:** 2253-2268.

del Giorgio, P. A., and T. C. Bouvier. 2002. Linking the physiologic and phylogenetic successions in free-living bacterial communities along an estuarine salinity gradient. *Limnology and Oceanography* **42:** p. 471-486.

del Giorgio, P. A., J. J. Cole, and A. Cimbleris. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductuve aquatic systems. *Nature* **385:** 148-151.

del Giorgio, P. A., and J. Davis. 2003. Patterns in dissolved organic matter lability and consumption across aquatic ecosystems. In: *Aquatic ecosystems: Interactivity of dissolved organic matter*, Findlay S. E. G., and R. L. Sinsabaugh [editors]. San Diego: Academic Press (Elsevier Science), p. 399-421

del Giorgio, P. A., and R. L. France. 1996. Ecosystem-specific patterns in the relationship between zooplankton and POM or microplankton $\delta^{13}C$. *Limnology and Oceanography* **41:** 359-365.

del Giorgio, P. A., and R. H. Peters. 1994. Patterns in planktonic P:R ratios in lakes: Influence of lake trophy and dissolved organic carbon. *Limnology and Oceanography* **39:** 772-787.

den Heyer, C., and J. Kalff. 1998. Organic matter mineralization rates in sediments: A within- and among-lake study. *Limnology and Oceanography* **43:** 695-705.

Denman, K. L., G. Brasseur, A. Chidthaison, P. Ciais, P. M. Cox, R. E. Dickinson, D. Hauglustaine, C. Heinze, E. Holland, D. Jacob, U. Lohmann, S. Ramachandran, P. L. da Silva Dias, S. C. Wosfy, and X. Zhang. 2007. Couplings between changes in the climate system and biogeochemistry. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Solomon, S., M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller (editors). Cambridge: Cambridge University Press, p. 500-587.

Dillon, P. J., and L. A. Molot. 1997. Dissolved organic and inorganic carbon mass balances in central Ontario lakes. *Biogeochemistry* **36:** 29-42.

Dubois, K., R. Carignan, and J. Veizer. 2009. Can pelagic net heterotrophy account for carbon fluxes from eastern Canadian lakes? *Applied Geochemistry* **24:** 988-998

Ellis, C. R., H. G. Stefan, and R. Gu. 1991. Water temperature dynamics and heat transfer beneath the ice cover of a lake. *Limnology and Oceanography* **36:** 324-335.

Fauteux, L., M. Cotrell, D. L. Krichman and P. A. del Giorgio. In prep. Temporal and spatial patterns in the abundance and cell-size of AAP bacteria in temperate and boreal lakes. Montréal, Université du Québec à Montréal, Département des Sciences biologiques.

Felip M., M. L. Pace, and J. J. Cole. 1996. Regulation of planktonic bacterial growth rates: The effects of temperature and resources. *Microbial Ecology* **31:** 15-28.

Ferland, M.-E. In prep. Étude du stockage de carbone des sediments lacustres en milieu tempéré et boreal du Québec, Thèse de Doctorat, Montréal, Université de Montréal, Département des Sciences biologiques.

France, R. L. 1995. Differenciation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnology and Oceanography* **40:** 1310-1313.

Fukushima, T., K. Matsushige, and R. S. J. Weisburd. 2000. Characteristics of nightime respiration in outdoor mesocosms. *Limnology* **1:** 159-170.

Gattuso, J.-P., S. Peduzzi, M.-D. Pizay, and M. Tonolla. 2002. Changes in freshwater bacterial community composition during measurements of microbial and community respiration. *Journal of Plankton Research* **24:** 1197-1206.

Granéli, W., M. Lindell, and L. Tranvik. 1996. Photo-oxidative production of dissolved inorganic carbon in lakes of different humic content. *Limnology and Oceanography* **41:** 698-706.

Guillemette, F., and P. A. del Giorgio. In press. Reconstructing the various facets of dissolved organic carbon bioavailability in freshwater ecosystems. *Limnology and Oceanography* (accepted, December 2010).

Hanson, P. C., D. L. Bade, S. R. Carpenter, and T. K. Kratz. 2003. Lake metabolism: relationships with dissolved organic carbon and phosphorus. *Limnology and Oceanography* **48:** 1112-1119.

Hecky, R. E., and R. H. Hesslein. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society* **14:** 631-653.

Hope, D., T. K. Kratz, and J. L. Riera. 1996. Relationship between pCO_2 and dissolved organic carbon in Northern Wisconsin lakes. *Journal of Environmental Quality* **25:** 1442-1445.

Houser, J. N., D. L. Bade, J. J. Cole, and M. L. Pace. 2003. The dual influences of dissolved organic carbon on hypolimnetic metabolism: organic substrate and photosynthetic reduction. *Biogeochemistry* **64:** 247-269.

Huotari, J., A. Ojala, E. Peltomaa, J. Pumpanen, P. Hari, and T. Vesala. 2009. Temporal variations in surface water CO_2 concentration in a boreal humic lake based on high-frequency measurements. *Boreal Environment Research* **14 (suppl. A):** 48-60.

Huttunen, J. T., J. Alm, A. Liikanen, S. Juutinen, T. Larmola, T. Hammar, J. Silvola, and P. J. Martikainen. 2003. Fluxes of methane, carbon dioxide and nitrous oxide in boreal lakes and potential anthropogenic effects on the aquatic greenhouse gas emissions. *Chemosphere* **52:** 609-621.

Jähne B., K. O. Münnich, R. B. A. Dutzi, W. Huber and P. Libner. 1987. On the parameters influencing air-water gas exchange. *Journal of Geophysical Research* **92:** 1937-1949.

Jonsson, A., J. Karlsson and M. Jansson. 2003. Sources of carbon dioxide supersaturation in clearwater and humic lakes in northern Sweden. *Ecosystems* **6:** 224-235.

Jonsson, A., M. Meili, A.-K. Bergström and M. Jansson. 2001. Whole-lake mineralization of allochthonous organic carbon in a large humic lake (Örträsket, N. Sweden). *Limnology and Oceanography* **46:** 1691-1700.

Kana, T. M., C. Darkangelo, M. D. Hunt, J. B. Oldham, G. E. Bennett and J. C. Cornwell. 1994. Membrane inlet mass spectrometer for rapid high-precision determination of N_2, O_2 and Ar in environmental water samples. *Analytical Chemistry* **66:** 4166-4170.

Karlsson, J., J. Ask and M. Jansson. 2008. Winter respiration of allochthonous and autochthonous organic carbon in a subarctic clear-water lake. *Limnology and Oceanography* **53:** 948-954.

Karlsson, J., M. Jansson, and A. Jonsson. 2007. Respiration of allochthonous organic carbon in unproductive forest lakes determined by the Keeling plot method. *Limnology and Oceanography* **52:** 603-608.

Keeling, C. D. 1958. The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas. *Geochimistry Cosmochimistry* **13:** 322-334.

Kelly, C. A., E. Fee, P. S. Ramlal, J. W. M. Rudd, R. H. Hesslein, C. Anema and E. U. Schindler. 2001. Natural variability of carbon dioxide and net epilimnetic production in the surface waters of boreal lakes of different sizes. *Limnology and Oceanography* **46:** 1054-1064.

Kling, G. W., G. W. Kipphut and M. C. Miller. 1991. Arctic lakes and streams as gas conduits to the atmosphere: implications for tundra carbon budgets. *Science* **251:** 298-301.

———————.. 1992. The flux of CO_2 and CH_4 from lakes and rivers in arctic Alaska. *Hydrobiologia* **240:** 23-36.

Kortelainen P., M. Rantakari, J. T. Huttunen, T. Mattsson, J. Alm, S. Juutinen, T. Larmola, J. Silvola and P. J. Martikainen. 2006. Sediment respiration and lake trophic state are important predictors of large CO_2 evasion from small boreal lakes. *Global Change Biology* **12:** 1554-1567.

Kritzberg, E. S., J. J. Cole, M. L. Pace, W. Granéli and D. L. Bade. 2004. Autochthonous versus allochthonous carbon sources of bacteria: Results from whole-lake ^{13}C addition experiments. *Limnology and Oceanography* **49:** 588-596.

Laudon, H., S. Köhler and I. Buffam. 2004. Seasonal TOC export from several boreal catchments in northern Sweden. *Aquatic Sciences* **66**: 223-230

Linsey, G. A., and D. C. Lasenby. 1985. Comparison of summer and winter oxygen consumption rates in a temperate dimictic lake. *Canadian Journal of Fisheries and Aquatic Sciences* **42:** 1634-1639.

Maberly, S. C. 1996. Diel, episodic and seasonal changes in pH and concentrations of inorganic carbon in a productive lake. *Freshwater Biology* **35:** 579-598.

Marchand, D. 2007. Relation entre les feux naturels, la respiration et les flux de CO_2 des lacs boréaux. Mémoire de maîtrise, Montréal, Université du Québec à Montréal, 65 p.

Marchand, D., Y. T. Prairie and P. A. del Giorgio. 2009. Linking forest fires to lake metabolism and carbon dioxide emissions in the boreal region of northern Québec. *Global Change Biology* **15:** 2861-2873.

Mathias, J. A., and J. Barica. 1980. Factors controlling oxygen depletion in ice-covered lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **37:** 185-194.

Matthews, D. A., and S. W. Effler. 2006. Long-term changes in the areal hypolimnetic oxygen deficit (AHOD) of Onondaga Lake: evidence of sediment feedback. *Limnology and Oceanography* **51:** 702-714.

Mattsson, T., P. Kortelainen and A. Räike. 2005. Export of DOM from boreal catchments: impacts of land use cover and climate. *Biogeochemistry* **76:** 373-394.

Maurice, C. F., T. Bouvier, J. Comte, F. Guillemette and P. A. del Giorgio. 2010. Seasonal variations of phage life strategies and bacterial physiological states in three northern temperate lakes. *Environmental Microbiology* **12:** 628-641.

McCallister, S. L., and P. A. del Giorgio. 2008. Direct measurement of the $\delta^{13}C$ signature of carbon respired by bacteria in lakes: Linkage to potential carbon sources, ecosystem baseline metabolism, and CO_2 fluxes. *Limnology and Oceanography* **53:** 1204-1216.

McKinney, C. R., J. M. McCrea, S. Epstein, H. A. Allen and H. C. Urey. 1950. Improvements in mass spectrometers for the measurement of small differences in isotope abundance ratio. *Review of Scientific Instruments* **21**: 724-730

Ministère des ressources naturelles et de la faune du Québec. 2003. Bref portrait de la forêt boréale au Québec. In *Gros plan sur le territoire et ses ressources*. En ligne. < http://www.mrnf.gouv.qc.ca/presse/feux-grands.jsp >. Consulté le 3 novembre 2010

Miyajima, T., Y. Yamada, E. Wada, T. Nakajima, T. Koitabashi, Y. T. Handa and K. Yoshii. 1997. Distribution of greenhouse gases, nitrite, and $\delta^{13}C$ of dissolved inorganic carbon in Lake Biwa: Implications for hypolimnetic metabolism. *Biogeochemistry* **36:** 205-221.

Molot, L. A., P. J. Dillon, B. J. Clark and B. P. Neary. 1992. Predicting end-of-summer oxygen profiles in stratified lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **49:** 2363-2372.

Murray, T. E., and P. H. Rich. 1995. Respiratory quotients predict increases in reducing products in the hypolimnion of a stratified lake. *Canadian Journal of Fisheries and Aquatic Sciences* **52:** 1183-1189.

Nedwell, D. B. 1999. Effect of low temperature on microbial growth: lowered affinity for substrates limits growth at low temperature. *FEMS Microbial Ecology* **30:** 101-111.

Nürnberg, G. K. 1995. Quantifying anoxia in lakes. *Limnology and Oceanography* **40:** 1100-1111.

Pace, M. L., and J. J. Cole. 2002. Synchronous variation of dissolved organic carbon and color in lakes. *Limnology and Oceanography* **47:** 333-342.

Pace, M. L., and Y. T. Prairie. 2005. Respiration in lakes. In *Respiration in Aquatic Ecosytems*, del Giorgio, P.A., and P. J. L. B. Williams [editors]. New York: Oxford University Press, p. 103-121.

Petrov, M. P., A. Y. Terzhevik, R. E. Zdorovennov, and G. E. Zdorovennova. 2007. Motion of water in an ice-covered shallow lake. *Water Resources And The Regime of Water Bodies* **34:** 131-140.

Prairie, Y. T. 2008. Carbocentric limnology: looking back, looking forward. *Canadian Journal of Fisheries and Aquatic Sciences* **65**: 543-548

Prairie, Y. T., D. F. Bird, and J. J. Cole. 2002. The summer metabolic balance in the epilimnion of southeastern Québec lakes. *Limnology and Oceanography* **47:** 316-321.

Rantakari, M., and P. Kortelainen. 2005. Interannual variation and climatic regulation of the CO_2 emission from large boreal lakes. *Global Change Biology* **11:** 1368-1380.

Raymond, P. A., and J. E. Bauer. 2000. Bacterial consumption of DOC during transport through a temperate estuary. *Aquatic Microbial Ecology* **22:** 1-12.

Ressources naturelles Canada. 2007A. Moyennes des précipitations totales (1971 à 2000). 1 : 7 500 000, In *Atlas du Canada*. En ligne. < http://atlas.nrcan.gc.ca/auth/francais/maps/environment/climate/precipitation/precip?layers=pcp_annual&map_web=TEMPLATE%20/home/atlas/mapdata/ajax.html&scale=42051275.911682&mapsize=428%20380&urlappend= >. Consulté le 3 novembre 2010

Ressources naturelles Canada. 2007B. Températures minimales et maximales quotidiennes moyennes pour le mois de janvier (1971 à 2000). 1 : 7 500 000, In *Atlas du Canada*. En ligne. < http://atlas.nrcan.gc.ca/auth/francais/maps/environment/climate/temperature/temp_winter/referencesandlinks.html/#references >. Consulté le 3 novembre 2010

Ressources naturelles Canada. 2007C. Températures minimales et maximales quotidiennes moyennes pour le mois de juillet (1971 à 2000). 1 : 7 500 000, In *Atlas du Canada*. En ligne. < http://atlas.nrcan.gc.ca/auth/francais/maps/environment/climate/temperature/temp_summer >. Consulté le 3 novembre 2010

Ressources naturelles Canada. 2009. Moyenne maximale d'épaisseur de neige (1979 à 1997). 1 : 7 500 000, In *Atlas du Canada*. En ligne. < http://atlas.nrcan.gc.ca/auth/francais/maps/environment/climate/snowcover/snowdepth >. Consulté le 3 novembre 2010

Rich, P. H. 1980. Hypolimnetic metabolism in three Cape Cod lakes. *American Midland Naturalist* **104:** 102-109

Riera, J. L., J. E. Schindler, and T. K. Kratz. 1999. Seasonal dynamics of carbon dioxide and methane in two clear-water lakes and two bog lakes in northern Wisconsin, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* **56:** 265-274.

Roehm C. L., Y. T. Prairie and P. A. del Giorgio. 2009. The pCO_2 dynamics in lakes in the boreal region of northern Québec, Canada. *Global Biogeochimical* Cycles **23:** doi: 10.1029/2008GB003297.

Sartory, D. P., and J. U. Groββelaar. 1984. Extraction of chlorophyll *a* from a freshwater phytoplankton for spectrophotometric analysis. *Hydrobiologia* **114:** 177-187

Schindler, D. W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos* **57:** 25-41.

Simon, M., and C. Wünsch. 1998. Temperature control of bacterioplankton growth in a temperate large lake. *Aquatic Microbial Ecology* **16:** 119-130.

Smith, V. H. 1979. Nutrient dependence of primary productivity in lakes. *Limnology and Oceanography* **24:** 1051-1064.

Sobek, S., G. Algesten, A.-K. Bergström, M. Jansson and L. J. Tranvik. 2003. The catchment and climate regulation of pCO_2 in boreal lakes. *Global Change Biology* **9:** 630-641.

Søndergaard, M., and M. Middelboe. 1995. A cross-system analysis of labile dissolved organic carbon. *Marine Ecology Progress Series* **118:** 283-294.

Striegl, R. G., P. Kortelainen, J. P. Chanton, K. P. Wickland, G. C. Bugna and M. Rantakari. 2001. Carbon dioxide partial pressure and ^{13}C content of north temperate and boreal lakes at spring ice melt. *Limnology and Oceanography* **46:** 941-945.

Striegl, R. G., and C. M. Michmerhuizen. 1998. Hydrologic influence on methane and carbon dioxide dynamics at two north-central Minnesota lakes. *Limnology and Oceanography* **43:** 1519-1529.

Tranvik, L. J., J. A. Downing, J. B. Cotner, S. A. Loiselle, R. G. Striegl, T. J. Ballatore, P. Dillon, K. Finlay, K. Fortino, L. B. Knoll, P. L. Kortelainen, T. Kutser, S. Larsen, I. Laurion, D. M. Leech, S. L. McCallister, D. M. McKnight, J. M. Melack, E. Overholt, J. A. Porter , Y. Prairie, W. H. Renwick, F. Roland, B. S. Sherman, D. W. Schindler, S. Sobek, A. Tremblay, M. J. Vanni, A. M. Verschoor, E. Von Wachenfeldt and G. A. Weyhenmeyer. 2009. Lakes and reservoirs as regulators of carbon cycling and climate. *Limnology and Oceanography* **54:** 2298-2314.

Tulonen, T. 1993. Bacterial production in a mesohumic lake estimated from [^{14}C]leucine incorporation rate. *Microbial Ecology* **26:** 201-217.

Vachon, D., and P. A. del Giorgio. In prep. Dynamique temporelle des processus menant à l'accumulation du CO_2 à la surface des lacs boréaux (Titre provisoire). Montréal, Université du Québec à Montréal, Département des Sciences biologiques.

Vadeboncoeur, Y., G. Peterson, M. J. V. Zanden and J. Kalff. 2008. Benthic algal production across lake size gradients: Interactions among morphometry, nutrients, and light. *Ecology* **89:** 2542-2552.

von Wachenfeldt, E., S. Sobek, D. Bastviken and L. J. Tranvik. 2008. Linking allochthonous dissolved organic matter and boreal lake sediment carbon sequestration: The role of light mediated flocculation. *Limnology and Oceanography* **53:** 2416-2426.

von Wachenfeldt, E., and L. J. Tranvik. 2008. Sedimentation in boreal lakes-The role of floccolation of allochthonous dissolved organic matter in the water column. *Ecosystems* **11:** 803-814.

Wanninkhof R. 1992. Relationship between wind speed and gas exchange over the ocean. *Journal of Geophysical Research* **97:** 7373-7382.

Wanninkhof R., and M. Knox. 1996. Chemical enhancement of CO_2 exchange in natural waters. *Limnology and Oceanography* **41:** 689-697.

Wanninkhof R., J. R. Ledwell, W. S. Broecker and M. Hamilton. 1987. Gas exchange on Mono Lake and Crowley Lake, California. *Journal of Geophysical Research* **92:** 14567-14580.

Welch H. E., and M. A. Bergmann. 1985. Winter respiration of lakes at Saqvaqjuac, N.W.T. *Canadian Journal of Fisheries and Aquatic Sciences* **42:** 521-528.

Welch, H. E., P. J. Dillon and A. Sreedharan. 1976. Factors affecting winter respiration in Ontario lakes. *Journal of the Fisheries Research Board of Canada* **33:** 1809-1815.

Wetzel, R. G., and G.E. Likens. 1991. Limnological analyses. New York: Springer Business +Media, 391 p.

Wharton, R. A., C. P. Mckay, G. D. Clow, and D. T. Andersen. 1993. Perennial ice covers and their influence on Antarctic lake ecosystems. *Antarctic Research Series* **ANTSA4 59:** 53-70.

White, D. M., H. M. Clilverd, A. C. Tidwell, L. Little, M. R. Lilly, M. Chambers and D. Reichardt. 2008. A tool for modeling the winter oxygen depletion rate in arctic lakes. *Journal of the American water resources association* **44**: 293-304

White, P. A., J. Kalff, J. B. Rasmussen and J. M. Gasol. 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. *Microbial Ecology* **21:** 99-118.

Williams, P. J. L. B., and P. A. del Giorgio. 2005. History and background. In *Respiration in Aquatic Ecosystems*, del Giorgio P. A., and P. J. l. B. Williams (editors.). New York: Oxford University Press, p. 1-17.